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THE UNIVERSITY OF ALBERTA

NATURE, GENETICS AND PHYSIOLOGY OF DOUBLE MUSCLED CATTLE

by

PAUL FELIX ARTHUR

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

IN

ANIMAL BREEDING AND GENETICS

DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA

SPRING 1990

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ABSTRACT

A series of studies was conducted, first, to examine the effects of the double muscled (DM) syndrome on various production traits and to partition these effects into those due to the DM genotype (direct transmitted effects) and those due to the DM dam (maternal effects), with the view of formulating feasible breeding strategies for the utilization of DM cattle. A second series of studies was conducted utilizing recombinant DNA technology to provide an initial characterization of the DM syndrome.

Data on 491 matings from a two-breed group diallel experiment involving DM and normal (N) cattle were used. The contributions of direct effects and maternal effects to the higher incidence of dystocia in DM cattle were equal. The conformation of the calf and the reduced size of the pelvic opening in DM cows were identified as the major factors involved in dystocia in DM cattle. Higher perinatal mortality of DM calves was attributed to direct effects, whereas the lower calf crop among DM cattle was the result of both direct and maternal effects. Growth of DM was slower than of N bull calves. DM bulls had higher values for muscling traits but lower values for fatness traits than N bulls. Maternal effects were small for growth traits and generally unimportant for carcass traits. Significant heterosis was obtained for most of the traits studied. The use of DM bulls as terminal sires on N cows is a reasonable approach to utilizing the DM syndrome in lean meat production. The incidence of dystocia from this mating type was similar to that of N matings, while the resultant male progeny had higher lean meat yield than their N

contemporaries.

Restriction site analysis of DNA from DM and N cattle did not show any differences between the two groups for growth hormone or insulin-like growth factor II genes. Although differences in circulating levels of growth hormone were obtained between DM and N cattle, these differences were related to differences in growth rate and body weight than to muscling, indicating that growth hormone might not be directly involved in the DM syndrome.

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I. GENERAL INTRODUCTION

Double muscling or muscular hypertrophy is an inherited condition which has been observed in many breeds of cattle. The name 'double muscle' is a misnomer since there is no duplication of muscles. The condition has been known under different names depending on geographic location, degree of hypertrophy and area of enlargement. It has been known under such names as culard, doppellender (double loin), a groppa dopia, double rumped, bottle thighed, greyhound belly, Yorkshire and Teeswater. The condition is a syndrome, implying that it is associated with many physical, physiological and histological characteristics other than muscular hypertrophy. The degree of expression of the syndrome varies with genetic background, environment, nutrition, sex and stage of maturity. Cattle showing the double muscled syndrome are characterized by hypertrophy of muscles especially in the regions of the proximal fore and hind quarters, protrusion of relatively visible muscles under the skin accompanied by depressions or intermuscular grooves (Menissier, 1982). Other physical characteristics include fineness of limb bones, higher frequency of occurence of animals with under developed external genetalia and enlarged tongues in newborn calves (Kieffer and Cartwright, 1980).

A. GENETICS

The double muscled (DM) syndrome in cattle was first documented by Cully in 1807 (cited by Oliver and Cartwright, 1968) Despite the fact that the knowledge of this syndrome has been in existence for a long time its mode of inheritance is still not known with certainty. The

variability in the expression of the DM character has been reported by many researchers. (Wriedt, 1929; Lauvergne, et al., 1963; Oliver and Cartwright, 1968; Menissier, 1982). The variable expression of this character has contributed to the uncertainty in the mode of inheritance of the DM trait. Most researchers agree that a pair of autosomal alleles at a single locus is involved in the inheritance of this character (Oliver and Cartwright, 1968; Logeay and Vissac, 1970; Rollins et al., 1972). There is, however, disagreement in the single gene pair hypothesis as to the mode of action of the gene. Some researchers (Dechambre, 1910, Wriedt, 1929 and Raimondi, 1962) believe that the gene involved in the inheritance of the DM character acts as a dominant gene. Other researchers (Weber and Ibsen, 1934; Kidwell et al., 1952, Oliver and Cartwright 1968; Kieffer et al., 1972; Kieffer and Cartwright, 1980; Hanset and Michaux, 1985a and b) however, believe the gene acts as a recessive. The different alternatives presented in the literature include partial dominance, incomplete recessiveness, incomplete penetrance and gene modifiers of some type. A dihybrid model, with nine possible genotypes expressed in four phenotypic classes was proposed by Sopena Quesada and Blanco Cachafeiro (1970). A trihybrid model was also proposed by Kronacher, 1934 (as cited by Rollins et al., 1972).

B. PHYSIOLOGY

Differences in muscle fibre type and number have been found between double muscled and normal cattle (Holmes and Ashmore, 1972; West, 1974). Differences between the two types of animals have also been observed in motor innervation of muscles (Swatland, 1973;

Novakofski et al., 1981), creatine and creatinine concentrations in the blood (Ansay and Hanset, 1979; Strath et al., 1981; Hanset and Michaux, 1982; Masoero, 1982), as well as in many other biochemical compounds. However, the fundamental physiological or biochemical alteration which is responsible for the double muscled syndrome is not known. While some researchers suggest that the primary abnormality may be due to an endocrine imbalance (Pomeroy and Williams, 1962; Vissac et al., 1974) others suggest that there is abnormality at the cell membrane level causing all these peculiar characteristics (King et al., 1976; Basarab et al., 1980).

C. REPRODUCTION

DM cattle show reduced fertility relative to normal cattle. It has been suggested that this is due to a number of factors including poor sexual behaviour (Vissac et al., 1974), especially at young ages (Oliver and Cartwright, 1968). Cases of genital infantilism and delays in puberty in heifers have been reported (Luciano, 1903; Vissac et al., 1974; Menissier, 1974). Delay in puberty as revealed by a reduced sexual odour and smaller testicles have also been reported in males (Kidwell et al., 1952; Dimitropoulos, 1972; Sanchez Garcia, 1976; Michaux and Hanset, 1981).

In mature males, although the amount of semen has been found to be smaller in volume, the number of spermatozoa is not substantially reduced (Sanchez Garcia, 1976). DM cows have also been found to exhibit reduced fertility (Vissac et al., 1974; Menissier et al., 1974). Calving difficulty and delay in puberty are partially responsible for the reduced fertility. Strath et al. (1981) reported

that cows showing muscular hypertrophy had similar estrus cycles to normal muscled ones and that heavy muscled cows which were cycling produced fertilizable ova and were capable of conceiving. However, Strath et al. (1981) observed that heavily muscled cows were less capable of carrying the fetus to term. Similar results were obtained by Rollins et al. (1972), who suggested a greater embryonic mortality in DM embryos. Chupin (1982) also believed that the losses might have occurred in the embryonic stage. Examination of the direct effects due to the DM embryos and maternal effects due to DM dams have not been comprehensively studied.

Higher frequency of dystocia in DM cattle is well documented. Menissier (1982) reported as much as 42 percent more caesarian sections performed in DM dams compared to normal dams. Calving difficulty in DM cattle is aptly described by Vissac et al., (1973) as a "foeto-maternal morphological imbalance at calving" leading to a greater incidence of calving difficulty. The problem is believed to be a combination of two factors: birth difficulties in DM calves (Dechambre, 1910; Wriedt, 1929; Vandeplassche et al., 1965; Vissac et al., 1973; Hanset and Jandrain, 1979) and parturition difficulties in DM dams (Kidwell et al., 1952; Vissac et al., 1973; Hanset and Jandrain, 1979).

The first consideration is a 'ponderal imbalance' (Menissier, 1982) between the lower calving weight of the dam (Vissac et al., 1973) and the higher birth weight of the calf (Vissac et al., 1973; Nott and Rollins, 1973; Hanset and Jandrain, 1979) which is not conducive to ease of calving. The second consideration is a 'morphological imbalance' at calving (Vissac et al., 1973). The

hypertrophy of the muscles of the thigh increases the width of the calf especially at the trochanters making delivery more difficult (McKellar, 1960; Vissac et al., 1973; Hanset and Jandrain, 1979). This situation is complicated by certain anatomical abnormalities believed to be of considerable frequency in DM females. Some researchers have observed a relative reduction of the skeleton of DM animals with maximum effect at the pelvic girdle (Vissac, 1968) plus the convergence of the iliac branches of the hip-bone (Derivaux et al., 1964; Fagot, 1964; Vissac, 1968) resulting in a notable narrowing of the pelvic opening of the dams. Inadequate behavioural preparation for calving by DM dams has also been suggested as contributing to the calving problems.

DM calves have often been reported as having poor viability (Hanset, 1967; Keiffer, et al., 1971). This seems to be the result of the poor adaptability of DM calves as well as the poor maternal performance of DM dams. The difficulties in calving result in a relatively weaker DM calf at birth. Compounded with this is the high incidence of deformities found in DM calves. Abnormalities such as enlarged tongues and rachitism are frequently found among DM calves (Hanset, 1961). Milk production in DM cows is said to be lower than in normal cows by 15 to 30 percent (Vissac et al., 1974). In breeds where the milk production of the cows is small the situation becomes even more critical for a DM dam of that breed to adequately nurse its calf.

There are some indications in the literature to suggest that the sex ratio of DM calves born does not follow the expected 1:1 ratio. Rollins et al., (1972) obtained a sex ratio of up to 5 males to 1 female and also cited the work of Smith, 1949; Kidwell et al., 1952;

Raimondi, 1963 and Hanset, 1967, all of whom obtained a significantly greater number of males than females in DM calves. Rollins et al., (1972) therefore suggested that a greater prenatal selection against DM females than against DM males may be responsible for this imbalance.

D. GROWTH

Many reports seem to indicate that DM cattle have higher birth weights than normal cattle (Hanset, 1967; Kieffer et al., 1971; Vissac et al., 1973; Nott, 1974). This increase in birth weight could be as high as 30 percent (Menissier, 1982). The higher growth rate of DM cattle continues to be manifested throughout the preweaning period (Dechambre, 1911; Carbone, 1940; Vissac et al., 1973). During the postweaning period however, some reports indicate that the growth rate of DM calves become inferior to that of normal calves and this results in a lower mature weight (Vissac, 1968; Vissac et al., 1973; Geay et al., 1982). In other reports, especially involving breeds with lower growth potential, DM cattle have been observed to maintain their growth superiority even during the postweaning period (Falliez, 1966; Trillat, 1967). The magnitude and direction of the differences in growth between DM cattle and normal cattle is subject to general factors such as management, maternal ability of dam, sex of calf and nutritional regime, which control the expression of the growth potential.

Most studies have reported a reduced appetite in DM cattle resulting in lower feed intake during the postweaning period (Trillat, 1967; Holmes and Ashmore, 1970; Geay et al., 1982). It is suggested

that the reduced feed intake is due to the reduction in the size of the digestive tract (Carbone, 1940; Vissac, 1968). Hence DM cattle express their growth potential better on concentrate diet. DM cattle tend to adapt less easily to feed restriction and dietary changes. Geay et al. (1982) found that DM cattle have better feed efficiency than normal cattle if the gain of muscles per unit energy intake is considered. However, restriction of feed up to 75% *ad libitum* reduced feed efficiency of DM bulls by 4.8 % but improved that of their normal Charolais and Friesian contemporaries by 9% and 15.5%, respectively.

Generally DM animals are more excitable or have a higher susceptibility to stress (Holmes et al., 1973; Halipre, 1973) and hence a reduced ability to adapt to herd management conditions than normal cattle. During forced exercise DM cattle show signs of fatigue faster than normal cattle (Holmes et al., 1973). The exhaustion is explained by Menissier (1982) as relating to metabolic acidosis due to a reduced blood circulation (lower blood volume and lower hematocrit count), leading to a deficiency in the transport of oxygen on the one hand and a reduction of the aerobic metabolic activity of the muscle of DM cattle on the other hand. During heat stress rectal temperatures of DM cattle increase more rapidly than normal cattle (Halipre, 1973; Strath, 1980). The large muscle mass of DM cattle results in abnormal or larger heat production during heat stress which is compounded by a lower capacity for heat dissipation (a reduction in respiratory capacity). High susceptibility to fasting stress has also been reported. Strath et al. (1980) observed that fasted DM bulls had elevated levels of cortisol and blood urea nitrogen compared to normal

bulls.

E. CARCASS CHARACTERISTICS

DM cattle are known to have superior carcass characteristics compared to normal cattle. This is mainly due to the generalized muscular hypertrophy, fineness of bones, lower potential to accumulate fat and smaller digestive tract of the DM cattle. The superiority of DM carcasses is reported to be mainly due to a higher dressing percentage and higher cutability and a larger proportion of muscle in the carcass and less bone (Oliver and Cartwright, 1968; West, 1974; Kauffman et al., 1976; Dumont, 1982; Geay et al., 1982: Shahin and Berg,1985). Thiessen (1974) reported up to 30% higher muscle:bone ratio in DM carcasses than in normal carcasses.

Modification to the body composition of DM animals is not uniform throughout the body. There are "highly hypertrophied", "hypertrophied" and even "hypotrophied" regions when comparisons between normal and DM cattle are made at constant muscle weight (Boccard and Dumont, 1974; Dumont, 1982; Shahin and Berg, 1985). In the rachidial region, the muscular hypertrophy seems to follow an anteroposterior gradient (Vissac, 1968) where the minimum hypertrophy will be located around the neck. Muscular hypertrophy is more marked in hindlimbs than in forelimbs (Vissac, 1968; Boccard and Dumont, 1974; Dumont, 1982). The muscular hypertrophy is also seen to affect peripheral muscles and those exhibiting a large superficial face (Pomeroy and Williams, 1962; Lohman et al., 1971; Boccard and Dumont, 1974). When looked at another angle, the muscular hypertrophy follows a distoproximal gradient (Butterfield, 1966; Hanset and Ansay, 1972)

and tends to be maximum at the level of the first brachial and crural segments (Boccard and Dumont, 1974). Bones of the limbs are subject to a reduction according to the same gradient (Vissac, 1968; Hanset and Ansay, 1972). Morphological differences in size and shape of long bones have been reported between DM and normal cattle. Wriedt (1929) found limb bones of DM cattle to be shorter and of decreased density. Vissac (1968) reported that shafts of long bones of DM cattle were more slender but had larger epiphyses. Hendricks et al. (1973) reported lighter and shorter bones that had thinner cortices in DM cattle.

While it is recognized that DM cattle have certain characteristics which limit production, the superior lean meat yield of DM cattle cannot be overlooked. Cattle showing the DM syndrome are used to a fair degree in crossbreeding systems in Europe, but their deliberate use in North America has been limited to a few research herds. The current consumer demand in North America, which is towards leaner meat, has increased the interest in the potential for utilization of DM cattle in commercial beef production. It is therefore essential to exploit the good production characteristics of the DM cattle. In order to formulate feasible breeding strategies to utilize the DM gene(s) in the short as well as the long term, certain aspects of the DM syndrome have to be investigated. Although it has been identified that research is needed to separate the effects of the DM syndrome into those due to the DM genotype (direct transmitted effects) and those due to the DM dams (maternal effects) (Menissier, 1982; Vissac, 1982), there has not been adequate research in this area. As well, with recent developments in molecular biology techniques, it is possible to examine further,

the DM syndrome at the molecular level, using such techniques as recombinant DNA technology. A series of studies was therefore undertaken to study the nature, genetics and physiology of the double muscled syndrome, with the view of evaluating the possible use of DM cattle in breeding programs under North American management systems in the short term as well as in the future.

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II. INCIDENCE OF DYSTOCIA AND PERINATAL CALF MORTALITY RESULTING FROM RECIPROCAL CROSSING OF DOUBLE MUSCLED AND NORMAL CATTLE[1]

A. INTRODUCTION

Double-muscling (DM), or muscular hypertrophy, is an inherited condition in cattle manifested by a generalized hypertrophy of muscles, a reduction in adipose tissue, plus a reduction in weight of the skeleton (Menissier, 1982; Shahin and Berg, 1985; Vissac, 1968). The DM conformation is characterized by hypertrophy of all muscles but particularly those in the proximal front and hind limbs, with clearly visible intermuscular grooving ascribed to a combination of massive muscular development and lack of subcutaneous fat (Menissier, 1982). DM cattle, therefore have higher than normal ratios of muscle to bone, muscle to fat, and expensive to cheaper cuts of meat (Shahin and Berg, 1985). Cattle showing the DM syndrome are, however, reported to show varying degrees of subfertility, higher incidence of calving difficulty, lower calf viability, and increased stress susceptibility (Menissier et al., 1974). This reported higher incidence of embryonic and calf mortality and dystocia may be attributable to the dam or the calf (Hanset and Jandrain, 1979). Different mating types between DM and normal (N) cattle should, therefore, result in different degrees of calving difficulty and calf mortality.

The objective of this study was to examine the incidence and causes of calving difficulty and perinatal calf mortality in the four possible mating types involving DM and N cattle.

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[1]A version of this chapter has been published. Arthur, P.F., M. Makarechian and M.A. Price. 1988. Can. Vet. J. 29:163.

B. MATERIALS AND METHODS

Calves showing the muscular hypertrophy syndrome have appeared in a hybrid herd of cattle at the University of Alberta ranch at Kinsella. The original herd was synthesized by crossing mainly Charolais, Angus, and Galloway breeds, and has been selected for growth rate and reproductive efficiency since 1961 (Berg et al., 1986). Cattle with the DM syndrome have been maintained and bred as a separate group at the ranch since 1967. The average breed composition of cows in the DM population at the beginning of this study was approximately 47 percent Angus, 14 percent each of Charolais, Galloway, and Hereford, and 11 percent other breeds. Cattle with at least fifty percent Hereford breeding were used as the normal (N) group.

Reciprocal crossings between the DM and N cattle were made for three breeding seasons starting in the summer of 1983 by mating DM x DM (bull x cow), DM x N, N x DM, and N x N (mating types). The DM bulls were all extreme in muscular development and the DM females showed various degrees of muscling but were all progeny of phenotypically DM bulls and cows from the DM herd. The breeding season was limited to July and August. Within each breeding season three DM and two N bulls were mated to an average of 33 DM and 87 N females at an average ratio of 24 females per bull in single sire matings. Approximately 14 percent of the females used in each mating type were heifers. A total of 348 matings were performed which resulted in 287 calvings. Cows and calves from the four mating types were treated identically.

Cows were wintered on the range, where some grazing was possible. Hay, straw, and grain supplement was provided depending on the severity of the winter and pasture conditions. Calving occurred in April and May each year. Dystocia was scored on a scale of zero to five, zero indicating unassisted calving and five representing Caesarian delivery. The scoring was done under the direction of a herdsman who had scored this trait on the same ranch every year since 1961. The calving scores were classified into three categories for this study as follows; calvings requiring slight or no assistance, calvings requiring mechanical aid such as the use of a puller, and calvings requiring a Caesarian section. Dystocias resulting from posterior presentation were also recorded. Records of stillbirths as well as calf mortalities within the first 48 hours after parturition were recorded. Calves were weighed and then scored subjectively for muscling at birth on a scale of zero to five with zero indicating normal muscling and five representing extreme double muscling. Dam's condition, scored subjectively on a scale of zero to five, and dam weight at calving were also recorded. In order to estimate area of pelvic opening, height and width of the pelvic opening in pregnant heifers and cows were measured by inserting a Rice Pelvimeter[2] into the rectum. Area of pelvic opening was defined as the product of the horizontal and vertical diameters. Pelvic measurements were taken from all pregnant cows (39 DM and 69 N) approximately two months before the start of the third calving season. These pelvic measurements were not taken prior to the earlier calving seasons.

Dystocia and perinatal mortality data were analyzed using analysis

[2]Lane Manufacturing Co., Denver, CO 80201.

of variance. Data for all the other traits were analyzed by least-squares procedures using a fixed model with mating type, year and age of dam as main effects (Harvey, 1985). This general model was modified for analysis of pelvic measurement data by using cow weight as a covariate. For birth weight data, sex of calf was included in the general model. Differences between means of traits which showed significant differences were tested using Student Newman Keul's Test (Steel and Torrie, 1980).

C. RESULTS AND DISCUSSION

Eighty - eight percent of all the calvings were normal or required slight assistance. Ten percent of the calvings required mechanical aid while only two percent required Caesarian section (Table II.1). DM x DM matings resulted in a significantly lower ($P<.05$) percentage of calvings requiring no or slight assistance compared with calvings resulting from DM x N and N x N matings. Twenty percent of calvings resulting from DM x DM matings required mechanical aid, which was significantly higher ($P<.05$) than those of calvings resulting from either DM x N or N x N matings. Differences in the percentage of calves delivered by Caesarian section in the four groups were not statistically significant ($P>.05$), but the numbers involved were small. In general, the incidence of dystocia was significantly higher ($P<.05$) in DM cows than N cows (19% vs 6%).

Other researchers have reported a higher incidence of calving difficulty in cows with muscular hypertrophy syndrome (Hanset and Jandrain, 1979; Menissier, 1982; Vissac et al., 1973). However, the

difference between DM and N cows observed in this study (19% vs 6%, respectively) was not as high as those reported by other researchers, such as Menissier (1982) who reported up to 210% more Caesarian sections in DM dams than in N dams. While the muscling type of the sire did not seem to affect the incidence of calving difficulty in normal cows, the muscling type of the sire seemed to have an effect on calving difficulty in the DM cows. Among the DM cows the incidence of dystocia was higher in cows bred to DM bulls than in cows bred to N bulls, although the difference was not statistically significant ($P>.05$).

In normal cattle, calf birth weight, age of cow, cow condition at calving and pelvic opening are traits reported to affect the incidence of calving difficulty (Makarechian et al., 1982). These traits were therefore examined in an attempt to explain the differences in the incidence of calving difficulty in the four mating types (Table II.2).

Calf birth weight, adjusted for sex effect, and cow condition at calving were not significantly different ($P>.05$) among the mating types and therefore could not have been responsible for the observed differences in calving difficulty (Table II.2). Significant differences ($P<.05$) in cow weight immediately after calving were observed. Cows from the N x DM mating type were the lightest at calving followed by cows from DM x DM, DM x N and N x N matings in that order. The order of average dam weight at calving did not correspond with the frequency of dystocia in the four mating types, indicating that other factors could be responsible for the observed differences in dystocia in the four groups. Calf birth weight as a percentage of dam weight at calving (calving index) has been shown to

be a fairly good predictor of dystocia, i.e. a higher index resulting in a higher probability of dystocia (Berg, 1979). However, in the present study, the maximum incidence of dystocia occurred among the DM cows mated to DM bulls, which had the minimum calving index among the four mating types. Therefore, differences in calf birth weight, cow weight, cow condition, and calving index could not explain the observed differences in the incidence of calving difficulty among the four mating types, indicating that among cows showing muscular hypertrophy, other factors such as conformation and area of pelvic opening may have considerable influence on calving performance.

The distribution of muscling scores of calves from the different mating types, at birth, is presented in Figure II.1. Forty-three percent of calves from DM x DM matings showed heavy muscling (scores greater than 2), while 9%, 12% and 0% of calves from DM x N, N x DM and N x N matings showed heavy muscling. Studies in normal populations of cattle suggest that the influence of calf conformation on dystocia is minimal after weight of calf effect has been considered (Meijering, 1984). The situation may well be different in DM cattle due to the extreme muscular development in these cattle. Some studies have suggested that hypertrophy of the muscles of the hindquarters increases the width of the DM calf, especially at the trochanters, thus making delivery of the fetus more difficult (Hanset and Jandrain, 1979; Vissac et al., 1973). The higher incidence of dystocia in mating types which gave rise to relatively more calves with muscular hypertrophy syndrome in this study supports this theory.

Another important factor which may contribute significantly to the higher incidence of dystocia in DM cows compared with N cows is the

area of pelvic opening. DM cows had smaller mean height and width of pelvic openings and thus smaller area of pelvic openings than the N cows when the weight of cow was used as a covariate in the model and the measurements adjusted for the age of dam ($P<.05$, Table II.3). These results support the observation by Vissac (1968) that in DM cows there is a relative reduction in the size of the pelvic girdle plus a convergence of the iliac branches of the hip-bones resulting in a notable narrowing of the pelvic opening.

Based on the results of this study it appears that the two major factors responsible for the observed differences in the incidence of calving difficulty among the four mating types are the conformation of the calf, and the reduced area of the pelvic opening in DM cows.

The overall perinatal calf mortality was 6.1 percent (Table II.4). DM x DM matings resulted in significantly higher ($P<.05$) mortality than either DM x N or N x N matings. Perinatal calf mortality as a result of N x DM matings was intermediate. Stillbirths occurred in 2.8 percent of all calvings with the highest value occurring as a result of DM x DM matings. The relatively higher incidence of stillbirths resulting from DM x DM matings could be attributed to the higher incidence of calving difficulty observed in DM x DM mating type compared with the other three mating types. Postpartum (within 48 hours of birth) mortality was also highest in DM x DM matings. Some of the DM x DM calves were observed to have enlarged tongues, a common component of the DM syndrome, making suckling difficult. Some of the DM dams were also observed to have enlarged teats or very little colostrum after calving. These abnormalities were also reported by Vissac et al. (1974). These abnormal conditions could at least partly

explain the low viability of calves resulting from DM x DM matings.

Based on the results of this study, matings of DM bulls to N cows will not result in any significant increase in the frequency of calf mortality or dystocia and could thus be further investigated as an alternative for lean meat production.

TABLE II.1 CALVING PERFORMANCE OF DOUBLE MUSCLED (DM) AND NORMAL (N) COWS USED IN RECIPROCAL CROSSING

Sire muscling type	Dam muscling type	No. of calvings	Percent of calvings requiring		
			Slight or no assistance	Mechanical aid	Caesarian section
DM	DM	40	78[b]	20*[a]	2*
DM	N	125	94[a]	5[b]	1
N	DM	34	85[ab]	12*[ab]	3
N	N	88	94[a]	4[b]	2
Total		287	88	10	2

*One calf within each group had posterior presentation.

[a,b]Means within the same column with different letters in their superscripts differ ($P<.05$).

TABLE II.2. LEAST-SQUARES MEANS AND STANDARD ERRORS FOR BIRTH WEIGHT, COW WEIGHT, CALVING INDEX, AND COW CONDITION SCORE IN DOUBLE MUSCLED (DM) AND NORMAL (N) CATTLE

Sire muscling type	Dam muscling type	No. of calvings	Calf birth wt, kg	Cow wt. after calving kg	Calving index[a]	Condition score
DM	DM	40	34.3 ± .9	438.4 ± 9.7[d]	8.0 ± .3[c]	3.3 ± .1
DM	N	125	36.0 ± .5	455.3 ± 4.9[c]	8.0 ± .1[c]	3.1 ± .1
N	DM	34	35.9 ± 1.0	406.9 ± 9.9[e]	9.3 ± .3[b]	3.2 ± .1
N	N	88	37.1 ± .5	461.3 ± 5.6[b]	8.2 ± .2[c]	3.2 ± .1

[a](Calf birth wt./cow wt. after calving) x 100.

b,c,d,e Means within the same column with different letters in their superscripts differ ($P<.05$).

TABLE II.3. LEAST-SQUARES MEANS AND STANDARD ERRORS OF PELVIC OPENING MEASUREMENTS[a] IN DOUBLE MUSCLED (DM) AND NORMAL (N) COWS

Muscling type	No. of cows	Height, cm	Width, cm	Area of pelvic opening, cm^2
DM	39	17.5 ± 0.1^{c}	16.4 ± 0.2^{c}	289.9 ± 4.3^{c}
N	69	18.1 ± 0.1^{b}	16.9 ± 0.1^{b}	306.5 ± 3.1^{b}

[a]Adjusted for weight and age of dam.

[b,c]Means within the same column with different letters in their superscripts differ ($P<.05$).

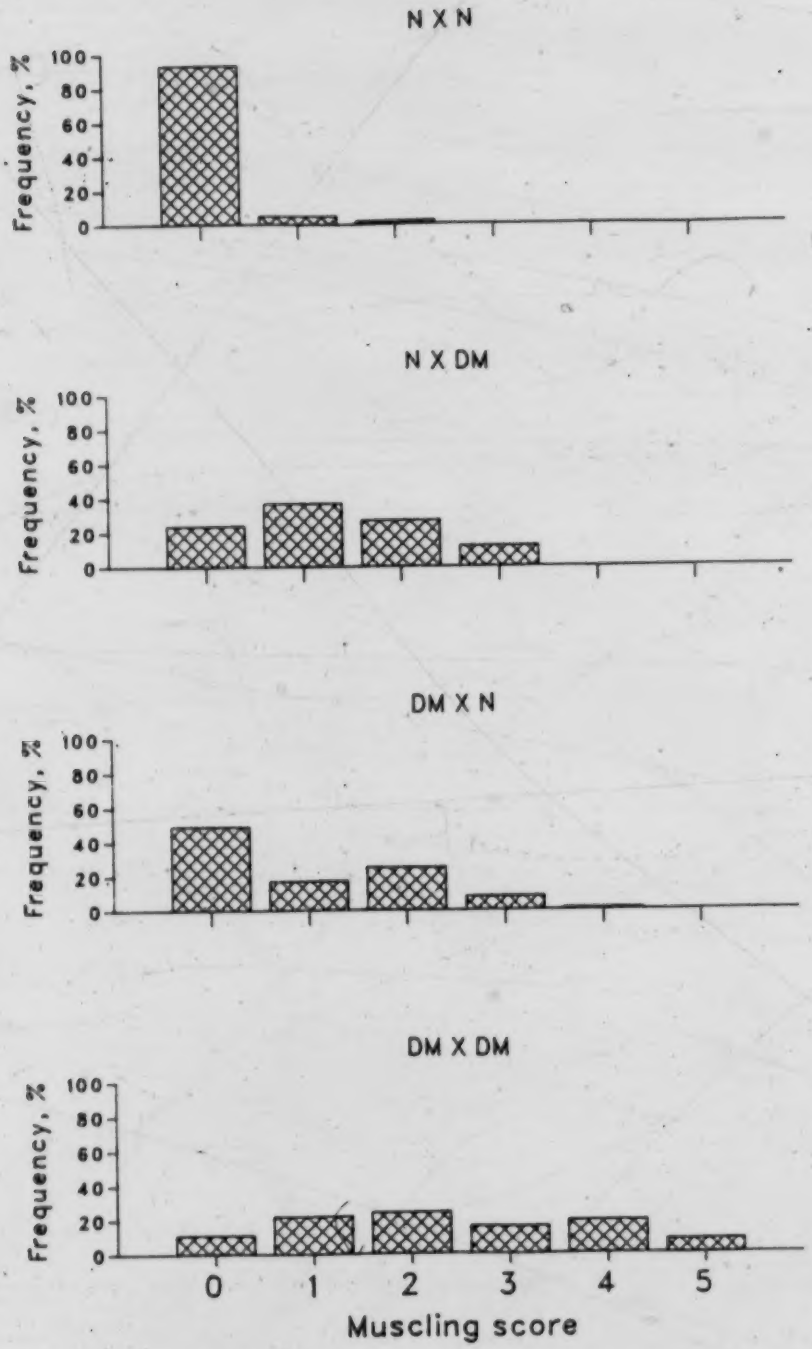
TABLE II.4. PERINATAL MORTALITY OF CALVES RESULTING FROM RECIPROCAL CROSSING OF DOUBLE MUSCLED (DM) AND NORMAL (N) CATTLE

Sire muscling type	Dam muscling type	No. of calvings	Stillbirths[a], %	Postpartum deaths[a], %	Overall perinatal mortality[a], %
DM	DM	40	5.0	7.5	12.5[b]
DM	N	125	.8	1.6	2.4[c]
N	DM	34	2.9	3.0	5.9[bc]
N	N	88	2.3	1.2	3.5[c]
Total		287	2.8	3.3	6.1

[a]As a percentage of total calvings within each mating type.

[b,c]Means within the same column with different letters in their superscripts differ ($P<.05$).

Figure II.1. Distribution of muscling score of calves at birth. 0 = normal muscling, 5 = extremely heavy muscling.


N X N
Frequency, %
100
80
60
40
20
0
N X DM
Frequency, %
100
80
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DM X N
Frequency, %
100
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60
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20
0
DM X DM
Frequency, %
100
80
60
40
20
0
0
1
2
3
4
5
Muscling score

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III. HETEROSIS, MATERNAL AND DIRECT EFFECTS IN DOUBLE-MUSCLED AND NORMAL CATTLE: I. REPRODUCTION AND GROWTH TRAITS[1]

A. INTRODUCTION

Double muscling or muscular hypertrophy is an inherited condition in cattle, postulated to be caused by a single autosomal gene, whose expression is influenced by modifier genes (Nott and Rollins, 1979; Menissier, 1982b). The syndrome is characterized by a generalized hypertrophy of muscles, a reduction in adipose tissue, and a reduction in weight of the skeleton (Vissac, 1968; Shahin and Berg, 1985). Compared to normal cattle, double-muscled (DM) cattle have less bone, less fat, more muscle, a higher muscle:bone ratio and a higher proportion of 'expensive' cuts of meat (Dumont, 1982; Menissier, 1982a; Shahin and Berg, 1985). Unfortunately the DM syndrome is associated with production problems such as reduced fertility, dystocia, low calf viability and increased stress susceptibility (Menissier et al., 1974; Arthur et al., 1988).

Breed differences, heterosis and maternal effects from beef cattle crossbreeding experiments have been shown to be important for reproduction traits and most measures of size (Gregory et al., 1978; Long, 1980; Dearborn et al., 1987). There has been limited work to characterize DM relative to normal cattle. This paper reports results of a double-muscled - normal cattle diallel experiment conducted to evaluate the importance of heterosis, maternal and direct transmitted effects on reproduction and growth traits.

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[1]A version of this chapter has been published. Arthur, P.F., M. Makarechian, M.A. Price and R.T. Berg. 1989. J. Anim. Sci. 67:902.

B. MATERIALS AND METHODS

In 1967 a Double-muscled (DM) cattle population was initiated at the University of Alberta ranch at Kinsella. Three DM bulls obtained from outside sources and one extreme-muscled bull from the Kinsella Beef Synthetic population (Berg et al., 1986) contributed to the introduction of 'double muscling' into the present DM herd. Initially cows bred to these DM bulls were normal Angus, Charolais and Galloway crossbreds. Since 1976, the DM herd has been bred as a closed breeding population, though it is open to extreme-muscled animals that arise in the other Kinsella herds. A detailed description of the DM population was given by Basarab (1981). The average breed composition of the DM breeding herd at the beginning of this study was approximately 47 percent Angus, 14 percent each of Charolais, Galloway and Hereford and 11 percent other breeds. A group of crossbred cattle that had at least 50 percent Hereford breeding with the remaining percentage made up of Angus, Charolais and Galloway, and showed no evidence of the DM condition were used as the normal (N) group.

Starting in the summer of 1983, reciprocal crossings of DM and N cattle were made over four breeding seasons (years), resulting in a total of 491 matings and 389 calvings. The number of observations by breed group of sire and breed group of dam subclass is presented in Table III.1. The DM bulls used were all extreme in muscular development (muscling score [described later] of 4 or 5) and the females (with muscling scores ranging from 3 to 5) were all progeny of phenotypically DM bulls and cows from the DM herd. In each breeding season, three DM and two N yearling bulls were used; each bull was

allotted 24 randomly chosen cows composed of both DM and N females in single-sire matings. Different bulls were used each breeding season except for one N and two DM bulls which were used two consecutive breeding seasons. The breeding herd was range-grazed all year round. Hay, straw and grain supplement were provided for 3 to 4 mo in the winter, the level and duration of feed supplementation were based on the severity of the winter. Breeding was in July and August and calvings occurred mainly in April and May the following year. Calvings requiring mechanical puller, veterinary assistance and caesarian section were classified as difficult calvings. Stillbirths and calf mortalities within the immediate 48 h of parturition were recorded as perinatal mortality. Calves were scored visually, at birth, for muscling on a scale of zero to five, with zero indicating normal muscling and five representing extreme muscular hypertrophy. Calves were not creep fed and remained with their dams on the range until weaning in October each year when the calves were approximately 6 mo old. After weaning, the male calves were weighed and placed in feedlot. A feedlot performance test was conducted for 140 d after an adjustment period of 28 d during which the calves were introduced to a high energy grain diet (Table III.2). Ad libitum feeding of the diet was continued until the cattle were shipped for slaughter. Live weights were recorded every month from weaning until slaughter. As the bulls approached finishing condition after the test, they were measured ultrasonically for backfat thickness between the 12th and 13th ribs on the right side of each animal at weekly intervals using a Scanogram[2].

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[2]Model 722, Ithaco, Ithaca, New York.

Whereas the data used for the evaluation of reproduction and preweaning traits covered four breeding seasons, only the data from the first three calving seasons were used for postweaning traits, because calves born in the fourth calving season were used in a different study. The female calves were put on a restricted diet after weaning. Because a restricted diet does not allow full expression of the true genetic potential of the animal, the data on postweaning growth of female calves were not presented in this report. For statistical analysis, calving difficulty, perinatal mortality and proportion of males were expressed as percentages of total calvings. Calf crop born and weaned were expressed as percentages of cows exposed. For each of these traits the occurrence of the effect (such as calving difficulty) was coded as 1 and the lack of occurrence (such as normal calving) as 0. After analysis, the resulting proportions were multiplied by 100 to obtain the percentages. Relative growth rate (RGR), as a measure of growth relative to instantaneous size, was computed as the difference between the natural logarithm of weaning and birth weights divided by the age at weaning (Fitzhugh and Taylor, 1971). The RGR, as used in this study, is the percentage of change in body weight per day. Weaning and yearling weights of all the cattle were adjusted to 180-d and 365-d weights, respectively. Backfat thickness measurements, which were taken at approximately 381 d of age, were used in the analyses.

The data were analyzed by least squares procedures using a mixed model (Harvey, 1985). The model included the fixed effects of breed group of sire, breed group of dam, year, age of dam (2, 3, 4 and 5 yr old and older), sex of calf and all possible two-way interactions.

Sires, within breed group of sire by year, were included in the model as random effects, and this mean square was used as the error term for testing significance of differences between sire breed groups, year, breed group of sire x year interaction, reciprocal cross differences and differences between straightbreds. Residual mean squares were used to test significance of other main effects and interactions, and heterosis. This model was used for all the traits except for calf crop traits, proportion of male calves and postweaning growth traits of male calves, where sex of calf and its interactions with the other factors were removed from the model.

The following linear contrasts of mating type least squares means were computed to characterize the breed groups:

Straightbred differences

$$(\text{DMxDM} - \text{NxN}) = [(G^{i}_{DM} + G^{m}_{DM}) - (G^{i}_{N} + G^{m}_{N})]$$

Heterosis (units)

$$1/2[(\text{DMxN} + \text{NxDM}) - (\text{DMxDM} + \text{NxN})] = H^{i}_{\text{DMxN}}$$

Maternal effect (Reciprocal cross differences)

$$(\text{NxDM} - \text{DMxN}) = (G^{m}_{DM} - G^{m}_{N})$$

Direct effect (Breed group of sire differences)

$$[(\text{DMxDM} + \text{DMxN}) - (\text{NxN} + \text{NxDM})] = (G^{i}_{DM} - G^{i}_{N}),$$

where G^{i} and G^{m} are direct and maternal effects, respectively, for the subscripted genetic group. The number of these contrasts exceeded the degrees of freedom, and hence the error over the entire set of comparisons may be different from that indicated by the probability level. However, the plan of the experiment was to estimate heterosis, additive maternal and additive direct effects, therefore the tests of

significance associated with these contrasts can be taken as guides (Gregory et al., 1978).

C. RESULTS

Differences Between Straightbreds

Differences between the straightbreds include differences between the DM and the N cattle in maternal and direct effects combined. The DM x DM matings resulted in a higher incidence of calving difficulty, perinatal mortality ($P<.01$) and higher proportion of males in the progeny ($P<.05$) compared to the N x N matings (Table III.3). Significant differences between the straightbreds in favour of the N x N matings also were obtained for all the calf crop traits, weight of calf weaned per cow exposed and all preweaning and postweaning growth traits (Tables III.4, III.5 and III.6). Difference between the straightbreds for calving date was not significant.

Heterosis

Individual heterosis was significant for calving difficulty and perinatal mortality (Table III.3). A negative heterosis of approximately 24 percent was obtained for each of these traits. Heterosis was not significant for the proportion of male calves in the progeny. Significant heterosis was observed for the percentages of calf crop born and calf crop weaned (Table III.4). Weight of calf weaned per cow exposed, which is a measure of herd productivity exhibited significant heterosis. The magnitudes of these effects were 6.4, 8.0 and 11.4 percent for calf crop born, calf crop weaned and

weight of calf weaned per cow exposed, respectively. Calving date did not show significant heterosis. Heterosis was significant for all preweaning and postweaning growth traits except for birth weight (Tables III.5 and III.6). Heterosis ranged from 5 to 8 percent for these traits, except for backfat thickness for which a 22 percent heterosis was observed.

Maternal Effects

Reciprocal cross difference (NxDM - DMxN; $G^m_{DM} - G^m_N$) reflects difference in maternal ability between DM and N cattle. Significant maternal effect was obtained for calving difficulty and proportion of males in the progeny (Table III.3). Maternal effect also was significant for the calf crop traits and weight of calf weaned per cow exposed (Table III.4). The DM females produced more male calves and had greater difficulty in calving, but they had a greater calf crop born and weaned. Overall efficiency was greater for the DM cows. Maternal effect for perinatal mortality and calving date was not significant. Whereas significant maternal effect was obtained for gain in the test period and for backfat thickness, maternal effect for all the other growth traits was not significant (Tables III.5 and III.6). For the significant growth traits, male progeny of DM females had higher values than those of N females.

Breed Group Direct Effects

Breed group of sire differences ($G^i_{DM} - G^i_N$) reflect one half of the differences in direct effects between DM and N breed groups. The DM breed group produced a higher incidence of calving

difficulty and perinatal mortality than did N breed group (P<.01, Table III.3). The N breed group produced a greater percentage of calves born and weaned and more weight at weaning per cow exposed than did the DM breed group, due to direct genetic effects (Table III.4). Breed group direct effects for calving date and proportion of males in the progeny were not significant. A significant direct effect also was observed for all the growth traits (Tables III.5 and III.6). For these traits the N-sired progeny had higher values than the DM-sired progeny.

The distribution of muscling scores at birth among the progeny of the four mating types is presented in Figure III.1. Based on a muscling score of 2 and above, the percentage of the progeny from DM x DM, DM x N and N x DM mating types showing a degree of muscling greater than normal were 77, 45 and 47 percent, respectively. Only 4 percent of the progeny from N x N matings showed some degree of heavy muscling.

D. DISCUSSION

The higher incidence of calving difficulty in DM than in N cattle is documented well (Hanset and Jandrain, 1979; Menissier, 1982a). This problem is believed to be caused by the conformation of the calf (hypertrophy of the muscles especially in the regions of the proximal fore and hind limbs) and the reduced size of the dam's pelvic opening (Hanset and Jandrain, 1979; Arthur et al., 1988). The significant maternal effect reflects the fact that calving problems were mainly attributable to the dam; therefore, the frequency of dystocia was

greatly reduced when DM sires were used on N cows instead of on DM cows. In an earlier study (Arthur et al., 1988; Chapter II) the higher incidence of dystocia in DM cattle was attributable to the reduced area of the pelvic opening in DM cows as well as to the conformation of the calf. Factors such as the occurrence of extremely muscular calves with enlarged tongues, which make suckling difficult, as well as DM cows with enlarged teats and very little colostrum, contributed to the low viability of DM calves (Vissac et al., 1974; Arthur et al., 1988).

There are some indications that the sex ratio among DM calves born does not follow the expected 1:1 ratio (Rollins et al., 1972). In the present study, the male:female ratio was 1.7:1 (significantly different from the expected 1:1 ratio) in calves born to the DM dams versus 1:1 in calves born to the N dams, irrespective of the breed group of sire. The biological reason for this imbalance in sex ratio is not known; it would be an interesting subject for research.

The DM cattle exhibit reduced fertility (Oliver and Cartwright, 1968; Strath, 1982). This has been attributed to a number of factors, including poor sexual behaviour, genital infantilism, delay in puberty and reduced sexual drive (Michaux and Hanset, 1981; Menissier, 1982a). It appears that both DM males and females are responsible for this subfertility (Menissier, 1982a). Milk production in DM cows also has been reported to be lower than in N cows (Vissac et al., 1974). Some or all of these factors could be responsible for the lower values for the calf crop traits in the DM compared to the N cattle. In this study reproductive problems appeared associated more with the males than with the females. The significant favourable heterosis for these

traits indicate that crossing between DM and N cattle results in significant improvement over DM x DM in the calf crop traits.

Although some reports indicate that DM cattle have superior growth potential compared to N cattle, other reports indicate that growth rate of DM calves is inferior to that of N calves, resulting in a lighter mature weight. In most of the British beef breeds, however, postweaning growth of DM calves has been reported to be slower than that of N calves (Nott and Rollins, 1979; Geay et al., 1982; Menissier, 1982a). The average breed composition of the DM breeding herd was 75 percent British (Angus, Hereford and Galloway). Selection of sires in the N breed group has been based on pre- and postweaning gain at the University of Alberta ranch (Berg et al., 1986). On the other hand, sire selection in the DM breed group has been based mainly on the extent of muscular hypertrophy of the individual bull and its parents. The difference in selection of sires between the N and DM breed groups could be partly responsible for the significant direct effect observed, whereby the progeny of N sires outperformed those of DM sires for all the growth traits.

Variability in the expression of the DM syndrome in the progeny of DM cattle and their crosses is documented well (West, 1974; Menissier, 1982b; Thiessen and Rollins, 1982). It is acknowledged that the magnitude of the effects obtained is dependent on the degree of expression of the DM syndrome. Hence reference should be made to the muscling scores, used as a measure of the degree of expression of the DM syndrome, in the intepretation of these results. Also, the estimates of the parameters may have been confounded with breed effect, because the genetic composition of the N and DM cattle was

different. Although similar breeds were present in both breed groups, the predominant breed in the DM herd was Angus (approximately 47%) compared with Hereford (approximately 60%) in the N herd.

TABLE III.1. NUMBER OF OBSERVATIONS WITHIN BREED GROUP OF SIRE AND BREED GROUP OF DAM SUBCLASS

	Breed group of sire								
	Double muscled			Normal			Total		
Breed group of dam	Cows exposed	Calves born	Calves weaned	Cows exposed	Calves born	Calves weaned	Cows exposed	Calves born	Calves weaned
Double muscled	81	57	49	62	53	50	143	110	99
Normal	213	165	153	135	114	109	348	279	262
Total	294	222	202	197	167	159	491	389	361

TABLE III.2. COMPOSITION OF GRAIN MIXTURE

Ingredients	Air dry composition
Barley, %	63
Oats, %	22
Alfalfa pellets, %	10
Canola meal, %	5
Total, %	100
Chemical Composition	*Per kg dry matter*
Dry matter, %	90.0
Digestible energy, MJ	14.2
Metabolizable energy, MJ	11.8
Protein, g	133.9
Acid detergent fibre, g	122.0
Calcium, g	5.7
Phosphorus, g	4.7
Salt, g	1.6

TABLE III.3. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR REPRODUCTION TRAITS: I

Item[a]	Calving difficulty, %	Perinatal calf mortality, %	Proportion of male calves[b]
Mating type means			
DM x DM	26.7 ± 3.9	13.4 ± 3.3	.63 ± .07
N x N	9.9 ± 2.8	4.6 ± 2.3	.51 ± .05
DM x N	9.5 ± 2.3	6.6 ± 2.0	.51 ± .04
N x DM	18.2 ± 4.1	7.0 ± 3.4	.65 ± .07
Straightbred differences			
$[(G^i_{DM} + G^m_{DM}) - (G^i_N + G^m_N)]$	16.8 ± .6**	8.8 ± .5**	.12 ± .06*
Heterosis (units)			
H^i_{DMxN}	-4.5 ± .3**	-2.2 ± .3**	.01 ± .05
Heterosis (%)	-24.6	-24.4	1.8
Maternal effect			
$(G^m_{DM} - G^m_N)$	8.7 ± .5**	.4 ± .5	.14 ± .06*
Direct effect			
$(G^i_{DM} - G^i_N)$	8.1 ± .8**	8.4 ± .7**	-.02 ± .08

[a]DM = Double muscled, N = Normal; sire breed group listed first.

[b]Males as a ratio of total number of calves born.

*,**Significant at P<.05 and P<.01, respectively.

TABLE III.4. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR REPRODUCTION TRAITS: II

Item[a]	Calving date[b]	Calf crop born, %	Calf crop weaned, %	Wt of calf weaned per cow exposed, kg
Mating type means				
DM x DM	112.6 ± 1.9	67.4 ± 4.9	59.7 ± 5.3	99.5 ± 10.5
N x N	112.3 ± 1.3	80.4 ± 3.6	77.3 ± 3.9	157.5 ± 7.7
DM x N	116.2 ± 1.1	75.9 ± 3.3	70.2 ± 3.5	132.7 ± 7.0
N x DM	111.5 ± 2.0	81.2 ± 3.6	77.8 ± 5.7	153.7 ± 11.3
Straightbred differences				
$[(G^{i}_{DM} + G^{m}_{DM}) - (G^{i}_{N} + G^{m}_{N})]$	0.3 ± 3.0	-13.0 ± .6**	-17.6 ± .6**	-58.0 ± 11.1**
Heterosis (units)				
H^{i}_{DMxN}	2.8 ± 2.9	4.7 ± .4**	5.5 ± .4**	14.7 ± 8.5*
Heterosis (%)	2.5	6.4	8.0	11.4
Maternal effect				
$(G^{m}_{DM} - G^{m}_{N})$	-4.7 ± 2.9	5.3 ± .6**	7.6 ± .6**	21.0 ± 11.4*
Direct effect				
$(G^{i}_{DM} - G^{i}_{N})$	5.0 ± 4.2	-18.3 ± .9**	-25.2 ± .8**	-79.0 ± 15.8**

[a]DM = Double muscled, N = Normal; sire breed group listed first.

[b]Number of days from January 1st to calving day.

*,**Significant at P<.05 and P<.01, respectively.

TABLE III.5. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR PREWEANING GROWTH TRAITS[a]

Item[b]	Birth wt, kg	Weaning wt, kg	ADG, kg/day	Relative growth rate, %/day
Mating type means				
DM x DM	31.9 ± .6	173.4 ± 4.2	.79 ± .02	.93 ± .02
N x N	36.7 ± .5	214.1 ± 2.8	.89 ± .01	1.02 ± .01
DM x N	34.7 ± .4	202.1 ± 2.4	.93 ± .01	1.04 ± .01
N x DM	34.8 ± .8	205.5 ± 4.2	.95 ± .02	1.03 ± .02
Straightbred differences				
$[(G^i_{DM} + G^m_{DM}) - (G^i_N + G^m_N)]$	-4.8 ± 1.1**	-40.7 ± 4.2**	-.20 ± .02**	-.09 ± .02**
Heterosis (units)				
H^i_{DMxN}	.5 ± .6	10.1 ± 3.2**	.05 ± .01**	.06 ± .01**
Heterosis (%)	1.5	5.2	5.6	6.2
Maternal effect				
$(G^m_{DM} - G^m_N)$	.1 ± 1.0	.4 ± 4.0	.02 ± .02	-.01 ± .02
Direct effect				
$(G^i_{DM} - G^i_N)$	-4.9 ± 1.5**	-41.1 ± 5.8**	-.22 ± .03**	-.08 ± .03*

[a]Based on data on both bull and heifer calves.

[b]DM = Double muscled, N = Normal; sire breed group listed first.

*,**Significant at P<.05 and P<.01, respectively.

TABLE III.6. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR POSTWEANING GROWTH TRAITS[a]

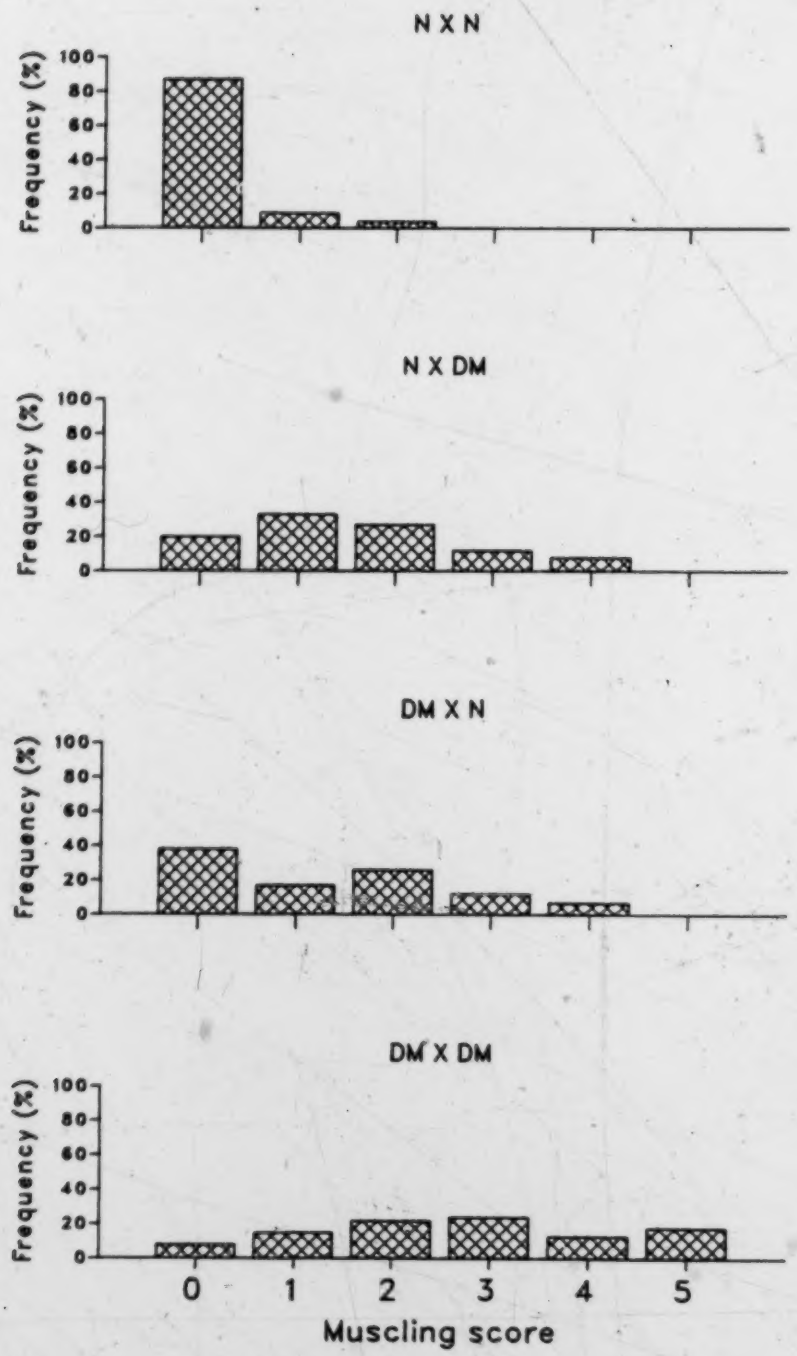
Item[b]	No.	Weaning wt, kg	Yearling wt, kg	Test period ADG, kg/day	Backfat thickness, mm
Mating type means					
DM x DM	24	178.1 ± 6.5	397.7 ± 11.7	1.39 ± .05	6.8 ± .5
N x N	40	225.3 ± 5.0	488.2 ± 9.0	1.68 ± .03	9.5 ± .4
DM x N	59	215.0 ± 4.5	464.0 ± 8.0	1.54 ± .03	8.6 ± .3
N x DM	20	214.8 ± 8.1	493.3 ± 14.5	1.75 ± .06	11.3 ± .6
Straightbred differences					
$[(G^i_{DM} + G^m_{DM}) - (G^i_N + G^m_N)]$		-47.2 ± 7.8**	-90.5 ± 15.9**	-.29 ± .06**	-2.7 ± .6**
Heterosis (units)					
H^i_{DMxN}		13.2 ± 5.5*	35.7 ± 9.9**	.11 ± .04**	1.8 ± .4**
Heterosis (%)		6.5	8.1	7.2	22.1
Maternal effect					
$(G^m_{DM} - G^m_N)$		-.2 ± 7.8	29.3 ± 15.9	.21 ± .05**	2.7 ± .6**
Direct effect					
$(G^i_{DM} - G^i_N)$		-47.0 ± 11.1**	-119.8 ± 22.5**	-.50 ± .08**	-5.4 ± .8**

[a]Based on data on bull calves only.

[b]DM = Double muscled, N = Normal; sire breed group listed first.

*,**Significant at P<.05 and P<.01, respectively.

Figure III.1. Distribution of muscling scores at birth among the progeny of the four mating types.
(0 = normal muscling, 5 = extremely heavy muscling).


N X N
N X DM
DM X N
DM X DM
Frequency (%)
100
80
60
40
20
0
0
1
2
3
4
5
Muscling score

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IV. HETEROSIS, MATERNAL AND DIRECT EFFECTS IN DOUBLE-MUSCLED AND NORMAL CATTLE: II. CARCASS CHARACTERISTICS OF YOUNG BULLS[1]

A. INTRODUCTION

Double muscling or muscular hypertrophy is an inherited condition in cattle manifested by a generalized hypertrophy of muscles, a reduction in fat deposition (Menissier, 1982; Shahin and Berg, 1985a) and a reduction in weight of the skeleton (Vissac, 1968). Double-muscled (DM) cattle therefore excel in carcass characteristics. Cattle showing the DM syndrome are, however, reported to show varying degrees of subfertility, calving difficulty, lower calf viability and increased stress susceptibility (Menissier et al., 1974; Vissac et al., 1974; Arthur et al., 1988). There has been renewed interest in the carcass characteristics of the DM cattle especially due to the fact that consumer demand in North America is moving toward leaner meat. However, information on the usefulness of DM cattle in breeding programs for lean meat production is limited. This paper, therefore, evaluates the importance of heterosis, additive maternal and direct transmitted effects for carcass traits, from a double-muscled - normal cattle diallel experiment.

B. MATERIALS AND METHODS

One hundred and thirty-five young bulls produced from three breeding seasons of reciprocal crossing of DM and normal (N) cattle in

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[1]A version of this chapter has been published. Arthur, P.F., M. Makarechian, M.A. Price and R.T. Berg. 1989. J. Anim. Sci. 67:911.

a diallel experiment were used in this study. Information on the management, breeding herd and breeding plan of the experiment was presented in detail by Arthur et al. (1989; chapter III). At about 1 yr of age, the bulls were scored visually for muscling on a scale of zero to five, with zero indicating normal muscling and five representing extreme muscular hypertrophy. As the bulls approached slaughter condition, they were measured ultrasonically for backfat thickness between the 12th and 13th ribs on the right side at weekly intervals using a Scanogram[2]. Based on the ultrasonic backfat thickness measurements bulls with an estimated backfat thickness of at least 4 mm (to ensure Canada grade A carcass) were shipped for slaughter a week later.

Bulls destined for slaughter were held for 24 hours without feed and water. All the bulls were trucked 150 km to a commercial packing plant in Edmonton for slaughter. Upon arrival at the packing plant each bull was weighed and slaughtered within a few hours. Carcasses were chilled (1 to 3°C) overnight after which carcass length was measured according to the method described by Yeates (1952). Agriculture Canada graders provided an appraisal for each carcass. The appraisal used was the standard ML 107 (blue tag) appraisal devised for Record of Performance testing, which consisted of a number of measurements including warm carcass weight, grade, meat color, marbling score (range 1 to 10, higher numbers representing less visible marbling), area of longissimus muscle (*m. longissimus thoracic*; "rib eye area") and fat cover at three positions over the longissimus muscle at the quartering (12-13th ribs) position

[2]Model 722, Ithaco, Ithaca, New York.

(subcutaneous fat thickness) and estimate of cutability. A 10-11-12th rib joint was removed from the right side of each carcass, trimmed according to the method described by Hankins and Howe (1946), and separated into fat, muscle and bone. Weight of each component was recorded and expressed as a percentage of the weight of the rib joint.

Two to three bulls from the DM x DM matings exhibiting extreme muscular hypertrophy were saved for use as breeding bulls each year. Thus, from the three calf crops, carcass data on eight DM x DM bulls were not available. This accounts for the eight fewer DM x DM bulls providing carcass data than the number [illegible]viding growth data for bulls (Arthur et al., 1989; chapter III). The [illegible]a were analyzed on an age constant basis, using age at slaughter as a covariate. The mean age at slaughter to which all data were adjusted was 398.5 days. The data were analyzed also on a weight constant basis, using either carcass weight or rib joint weight as a covariate. The mean carcass and rib joint weights to which the data were adjusted were 303.3 kg and 4812 g, respectively.

The data were analyzed by least squares procedures using a mixed model (Harvey, 1985). The model included the fixed effects of breed group of sire, breed group of dam, year, age of dam and all possible two-way interactions. Sires, within breed group of sire by year, were included in the model as random effect, and this error mean square was used as the error term for testing significance of differences between sire breed groups, year, breed group of sire x year interaction, reciprocal cross differences and differences between the straightbreds. Residual mean squares were used to test significance of other main effects, interactions and heterosis. The following linear

contrasts of mating type least squares means were computed to characterize the breed groups:

Straightbred differences

$$(DMxDM - NxN) = [(G^{i}_{DM} + G^{m}_{DM}) - (G^{i}_{N} + G^{m}_{N})]$$

Heterosis (units)

$$1/2[(DMxN + NxDM) - (DMxDM + NxN)] = H^{i}_{DMxN}$$

Maternal effect (Reciprocal cross differences)

$$(NxDM - DMxN) = (G^{m}_{DM} - G^{m}_{N})$$

Direct effect (Breed group of sire differences)

$$[(DMxDM + DMxN) - (NxN + NxDM)] = (G^{i}_{DM} - G^{i}_{N}),$$

where G^{i} and G^{m} are direct and maternal effects, respectively, for the subscripted genetic group.

C. RESULTS

COMPARISONS ON AGE CONSTANT BASIS

Differences Between Straightbreds

Differences between the straightbreds include differences between the DM and N cattle in maternal and direct effects combined. The N straightbreds had significantly higher values than DM straightbreds for slaughter and carcass weights, subcutaneous fat thickness (Table IV.1) and carcass length (Table IV.2). The DM straightbreds, however, had higher ($P<.05$) dressing percentage and higher ($P<.01$) percent estimated cutability than N straightbreds. Differences between the straightbreds for marbling score and rib eye area were not

significant.

For traits measured using the rib joint, N straightbreds had significantly higher values than DM straightbreds for rib joint weight, fat weight and percentage (Table IV.3), and bone weight (Table IV.4). The DM straightbreds had higher ($P<.01$) percentage of muscle and muscle:fat ratio, as well as higher ($P<.05$) muscle:bone ratio. Differences between the straightbreds for muscle weight and percentage of bone were not significant.

Heterosis

Significant heterosis of 8.7 and 6.8 percent was obtained for slaughter and warm carcass weights, respectively (Table IV.1). Heterosis of -2.3 percent for dressing percentage was observed ($P<.01$). Significant positive heterosis was obtained for subcutaneous fat thickness and carcass length (Table IV.2). Heterosis for estimated cutability, marbling score and rib eye area was not significant.

Significant heterosis was observed for the weights of the 10-11-12th rib joint, fat, muscle (Table IV.3) and bone (Table IV.4). Although heterosis for percentage of muscle was not significant, 6.6 and -7.7 percent heterosis was obtained for percentage fat ($P<.05$) and percentage of bone ($P<.01$); respectively. Heterosis of -31 percent was obtained for muscle:fat ratio ($P<.01$), whereas an 8.1 percent heterosis was obtained for muscle:bone ratio ($P<.01$).

Maternal Effects

Reciprocal cross differences (NxDM - DMxN; $G^m_{DM} - G^m_N$) reflect differences in maternal ability between DM and N cattle. A

significant maternal effect was obtained only for subcutaneous fat thickness and rib joint weight. For both traits, progeny of the N x DM matings had larger values than those from the DM x N matings.

Breed Group Direct Effects

Breed group of sire differences ($G^i_{DM} - G^i_N$) reflect one half of the differences in direct effects between DM and N breed groups. Significant direct effect was obtained for slaughter and carcass weights, subcutaneous fat thickness and carcass length (Table IV.1). The N sires produced higher values than DM sires for each of these traits. The DM sires, however, contributed to a higher dressing percentage ($P<.05$) and percent cutability ($P<.01$). Breed group direct effects were not significant for marbling score and rib eye area.

For the rib joint measurements, direct effect was significant for the rib joint weight, fat weight and percentage and bone weight (Table IV.2). The N sires had higher values than DM sires for each of these traits. Percentage of muscle, muscle:fat and muscle:bone ratios were higher ($P<.01$) in the progeny of DM sires than in those of N sires (Tables IV.3 and IV.4). No significant direct effect was obtained for muscle weight and percentage of bone.

COMPARISONS ON WEIGHT CONSTANT BASIS

When the carcass data were adjusted to a common carcass weight, heterosis for all the traits except subcutaneous fat thickness and carcass length was similar to those obtained on an age constant basis (Tables IV.5 and IV.6). Heterosis for subcutaneous fat thickness and carcass length although significant on an age constant basis was not

significant when the data were adjusted for weight differences. Adjusting the rib joint measurements to a common rib joint weight resulted in significant positive heterosis only for percentage of muscle (Table IV.7 and IV.8).

Maternal effect was important only for subcutaneous fat thickness where the progeny of N x DM had higher ($P<.05$) values than the progeny of DM x N crosses. Breed group direct effects and differences between straightbreds on the weight constant basis were similar to those obtained on the age constant basis except for the difference in rib eye area. Carcasses from DM-sired progeny and DM straightbred had larger rib eye areas than those from the N-sired progeny and N straightbreds, respectively.

The distribution of muscling scores among the male progeny from the four mating types measured at approximately 1 yr of age is presented in Figure IV.1. Whereas sixty percent of all male progeny from DM x DM matings were very heavily muscled (muscling score of 3 and above), fifteen, thirty-eight and two percent of male calves from DM x N, N x DM and N x N matings, respectively, were heavily muscled.

D. DISCUSSION

For most of the traits studied, the relative importance of the various effects remained unchanged when the data were adjusted for age or weight differences. This indicates that there are important genetic differences among the breed groups as well as the crosses for these traits in which the influences of age or weight are similar. Heterosis estimated on an age constant basis for subcutaneous fat thickness and

carcass length was influenced by variation in body weight because when the data were adjusted for carcass weight these effects were not significant. Breed group direct effect and differences between the straightbreds were evident for rib eye area adjusted to a constant carcass weight but disappeared when assessed at a constant age of 398.5 days. The DM x DM carcasses were about 80 kg lighter than N x N carcasses.

Cattle showing the DM syndrome are characterized by generalized muscular hypertrophy, fineness of bones, lower potential to accumulate fat and smaller digestive tract (Oliver and Cartwright, 1968; Menissier, 1982). These characteristics result in a higher dressing percentage, higher cutability and a higher proportion of muscle in the carcass and less bone (Dumont, 1982; Shahin and Berg, 1985a). Results obtained in this study are in agreement generally with those published in the literature. On a weight constant basis, DM x DM carcasses had 7 % higher dressing percentage and 14 percent larger rib eye areas than N x N carcasses. Rib joints from DM x DM carcasses had 22 % less fat, 15 % more muscle and 24 % higher muscle:bone ratio than those from N x N carcasses. The degree of hypertrophy of muscles in the DM animal is not uniform throughout the body. Muscular hypertrophy seems to follow an anterioposterior gradient (Vissac, 1968), where the minimum hypertrophy is located around the neck, and a distoproximal gradient (Butterfield, 1966; Hanset and Ansay, 1972). Shahin and Berg (1985b), working with cattle from the same herd as that used in this study, reported that muscles associated with the 10-11-12th rib joint were only moderately hypertrophied, hence they might be considered as representative of the DM carcass as a whole.

The magnitude of the effects reported is dependent on the degree of expression of the DM syndrome. Reference to the muscling scores therefore should be made in the interpretation of these results. As well, because the DM and N cattle used did not have similar breed composition, the parameters estimated may have been confounded with breed effects.

The significant heterosis effects for carcass traits observed in this study suggest that significant favourable gains can be made, especially in muscling and leanness traits, by crossing DM and N cattle. Results of work reported by Rollins et al. (1980) in the United States, working with DM x N and N x N cattle, showed similar gains from crossing DM and N cattle. Maternal effects generally were unimportant for carcass traits evaluated in this study, therefore, either of the reciprocal crosses will yield favourable carcass composition. Maternal effect for growth was small. However, whereas N x DM matings resulted in higher incidence of calving difficulty compared with DM x N matings, DM x N matings resulted in lower calf crop. (Arthur et al., 1989; chapter III). It might be easier to improve calf crop in DM x N matings through the use of few, fertile DM bulls by artificial insemination (to prevent reductions in calf crop due to reduced libido) than to reduce calving difficulty in the N x DM matings. As well, considering other factors such as stress susceptibility of DM cattle (Menissier, 1982), which was not investigated in this study, it might be cheaper to maintain N instead of DM breeding cows. Therefore the use of DM sires on N females may be a reasonable approach in the attempt to utilize the desireable carcass characteristics of DM cattle.

TABLE IV.1. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR CARCASS TRAITS (AGE CONSTANT BASIS: I)

Item[a]	No.	Slaughter wt, kg	Warm carcass wt, kg	Dressing percentage	Subcutaneous fat, mm
Mating type means					
DM x DM	16	429.2 ± 13.6	269.2 ± 8.5	63.2 ± .7	7.5 ± .7
N x N	40	510.2 ± 8.7	305.1 ± 5.4	59.8 ± .4	12.6 ± .5
DM x N	59	498.7 ± 7.8	299.8 ± 4.9	60.2 ± .4	10.1 ± .4
N x DM	20	522.2 ± 14.2	313.4 ± 8.9	60.0 ± .7	12.3 ± .8
Straightbred differences					
$[(G^i_{DM} + G^m_{DM}) - (G^i_N + G^m_N)]$		-81.0 ± 20.3**	-35.9 ± 10.2**	3.4 ± 1.2*	-5.1 ± .9**
Heterosis (units)					
H^i_{DMxN}		40.8 ± 10.2**	18.5 ± 6.4**	-1.4 ± .5**	1.2 ± .6*
Heterosis (%)		8.7	6.8	-2.3	11.9
Maternal effect					
$(G^m_{DM} - G^m_N)$		23.5 ± 17.8	13.6 ± 8.9	-.2 ± 1.0	2.2 ± .8*
Direct effect					
$(G^i_{DM} - G^i_N)$		-104.5 ± 27.0**	-49.5 ± 13.5**	3.6 ± 1.5*	-7.3 ± 1.2**

[a]DM = Double muscled, N = Normal; sire breed group listed first.

*,**Significant at P<.05 and P<.01, respectively.

TABLE IV.2. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR CARCASS TRAITS (AGE CONSTANT BASIS: II)

Item[a]	No.	Cutability, %	Marbling score	Rib eye area, cm^2	Carcass length, cm
Mating type means					
DM x DM	16	61.3 ± .4	8.0 ± .2	90.5 ± 2.6	112.7 ± 1.4
N x N	40	58.5 ± .3	7.5 ± .1	83.5 ± 1.7	120.2 ± .9
DM x N	58	60.3 ± .2	7.5 ± .1	92.1 ± 1.5	118.2 ± .8
N x DM	20	59.5 ± .4	7.5 ± .1	89.7 ± 2.7	120.1 ± 1.4
Straightbred differences					
$[(G^i_{DM} + G^m_{DM}) - (G^i_N + G^m_N)]$		2.8 ± .6**	.5 ± .2	7.0 ± 4.0	-7.5 ± 1.6**
Heterosis (units)					
H^i_{DMxN}		.0 ± .6	-.5 ± .2	7.8 ± 3.8	3.2 ± 1.0**
Heterosis (%)		.0	-6.5	9.0	2.8
Maternal effect					
$(G^m_{DM} - G^m_N)$		-.8 ± .6	.0 ± .1	-2.4 ± 3.5	.9 ± 1.4
Direct effect					
$(G^i_{DM} - G^i_N)$		3.6 ± .9**	.5 ± .2	9.4 ± 5.4	-8.4 ± 2.2**

[a]DM = Double muscled, N = Normal; sire breed group listed first.

*,**Significant at P<.05 and P<.01, respectively.

TABLE IV.3. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR RIB JOINT DISSECTION TRAITS (AGE CONSTANT BASIS: I)

Item[a]	No.	Rib joint	Fat		Muscle	
		wt, g	Wt, g	%	Wt, g	%
Mating type means						
DM x DM	16	3838 ± 163	936 ± 78	22.8 ± 1.2	2318 ± 100	61.6 ± 1.1
N x N	40	4866 ± 105	1584 ± 50	32.1 ± .7	2535 ± 64	52.4 ± .7
DM x N	59	4792 ± 83	1355 ± 44	28.0 ± .7	2746 ± 57	57.4 ± .6
N x DM	20	5147 ± 171	1567 ± 81	30.4 ± 1.2	2857 ± 105	55.5 ± 1.1
Straightbred differences						
$[(G^i_{DM} + G^m_{DM}) - (G^i_N + G^m_N)]$		-1028 ± 156**	-648 ± 111**	-9.3 ± 2.3**	-217 ± 148	9.2 ± 2.3**
Heterosis (units)						
H^i_{DMxN}		617 ± 123**	201 ± 59**	1.8 ± .9*	375 ± 75**	-.6 ± .8
Heterosis (%)		14.2	16.0	6.6	15.5	-1.1
Maternal effect						
$(G^m_{DM} - G^m_N)$		355 ± 137*	212 ± 97	2.4 ± 2.0	111 ± 130	-1.9 ± 2.0
Direct effect						
$(G^i_{DM} - G^i_N)$		-1383 ± 208**	-860 ± 148**	-11.7 ± 3.0**	-328 ± 197	11.1 ± 3.0**

[a]DM = Double muscled, N = Normal; sire breed group listed first.

*,**Significant at P<.05 and P<.01, respectively.

TABLE IV.4. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR RIB JOINT DISSECTION TRAITS (AGE CONSTANT BASIS: II)

Item[a]	No.	Bone		Muscle:fat	Muscle:bone
		Wt, g	I		
Mating type means					
DM x DM	16	581 ± 24	15.6 ± .4	4.0 ± .3	4.0 ± .1
N x N	40	740 ± 15	15.4 ± .3	1.8 ± .2	3.4 ± .1
DM x N	59	687 ± 14	14.5 ± .2	2.2 ± .2	4.0 ± .1
N x DM	20	722 ± 25	14.2 ± .4	1.9 ± .3	4.0 ± .1
Straightbred differences					
$[(G^i_{DM} + G^m_{DM}) - (G^i_N + G^m_N)]$		-159 ± 32**	.2 ± .3	2.2 ± .4**	.6 ± .1*
Heterosis (units)					
H^i_{DMxN}		44 ± 18*	-1.2 ± .3**	-.9 ± .2**	.3 ± .1**
Heterosis (I)		6.7	-7.7	-31.0	8.1
Maternal effect					
$(G^m_{DM} - G^m_N)$		35 ± 28	-.3 ± .2	-.3 ± .3	.0 ± .1
Direct effect					
$(G^i_{DM} - G^i_N)$		-194 ± 43**	.5 ± .4	2.5 ± .5**	.6 ± .2*

[a]DM = Double muscled, N = Normal; sire breed group listed first.

*,**Significant at P<.05 and P<.01, respectively.

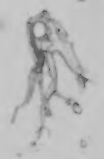


TABLE IV.5. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR CARCASS TRAITS (CARCASS WEIGHT CONSTANT BASIS: I)

Item[a]	No.	Age at slaughter, d	Slaughter wt, kg	Dressing percentage	Subcutaneous fat, mm
Mating type means					
DM x DM	16	408.0 ± 4.5	479.6 ± 6.0	63.8 ± .7	8.1 ± .8
N x N	40	394.7 ± 2.7	508.1 ± 3.6	59.8 ± .4	12.6 ± .5
DM x N	59	398.1 ± 2.4	504.4 ± 3.2	60.2 ± .4	10.2 ± .4
N x DM	20	392.7 ± 4.5	507.9 ± 5.9	59.8 ± .7	12.2 ± .8
Straightbred differences					
$[(G^i_{DM} + G^m_{DM}) - (G^i_N + G^m_N)]$		13.3 ± 7.2	-28.5 ± 10.2*	4.4 ± 1.2**	-4.5 ± 1.0**
Heterosis (units)					
H^i_{DMxN}		-11.9 ± 6.3	12.3 ± 4.2**	-1.8 ± .5**	.9 ± .6
Heterosis (%)		-3.0	2.5	-2.9	8.7
Maternal effect					
$(G^m_{DM} - G^m_N)$		-5.4 ± 6.4	3.5 ± 8.9	-.4 ± 1.1	2.0 ± .9*
Direct effect					
$(G^i_{DM} - G^i_N)$		18.7 ± 9.6	-32.0 ± 13.6*	4.4 ± 1.6*	-6.5 ± 1.3**

[a]DM = Double muscled, N = Normal; sire breed group listed first.

*,**Significant at P<.05 and P<.01, respectively.

TABLE IV.6. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR CARCASS TRAITS (CARCASS WEIGHT CONSTANT BASIS: II)

Item[a]	No.	Cutability, %	Marbling score	Rib eye area, cm^2	Carcass length, cm
Mating type means					
DM x DM	16	61.6 ± .5	7.9 ± .2	95.0 ± 2.5	116.6 ± 1.1
N x N	40	58.5 ± .3	7.5 ± .1	83.3 ± 1.5	120.1 ± .6
DM x N	59	60.3 ± .2	7.5 ± .1	92.6 ± 1.4	119.6 ± .6
N x DM	20	59.4 ± .4	7.5 ± .2	88.5 ± 2.5	119.0 ± 1.0
Straightbred differences					
$[(G^i_{DM} + G^m_{DM}) - (G^i_N + G^m_N)]$		3.1 ± .6**	.4 ± .2	11.7 ± 3.6**	-3.5 ± 1.1*
Heterosis (units)					
$H^i_{DM \times N}$		-.2 ± .3	-.4 ± .2	1.4 ± 1.8	1.0 ± .7
Heterosis (%)		-.3	-5.2	1.6	.8
Maternal effect					
$(G^m_{DM} - G^m_N)$		-.9 ± .5	.0 ± .1	-4.1 ± 3.1	-.6 ± 1.0
Direct effect					
$(G^i_{DM} - G^i_N)$		4.0 ± .8**	.4 ± .2	15.8 ± 4.8**	-2.9 ± 1.5

[a]DM = Double muscled, N = Normal; sire breed group listed first.

*,**Significant at P<.05 and P<.01, respectively.

TABLE IV.7. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR RIB JOINT DISSECTION TRAITS (RIB JOINT WEIGHT CONSTANT BASIS: I)

Item[a]	No.	Fat		Muscle	
		Wt, g	%	Wt, g	%
Mating type means					
DM x DM	16	1248 ± 59	24.8 ± 1.3	2834 ± 59	60.5 ± 1.2
N x N	40	1565 ± 33	32.0 ± .7	2507 ± 33	52.5 ± .7
DM x N	59	1362 ± 29	28.0 ± .6	2757 ± 29	57.4 ± .6
N x DM	20	1448 ± 55	29.7 ± 1.2	2680 ± 54	55.9 ± 1.1
Straightbred differences					
$[(G^{i}_{DM} + G^{m}_{DM}) - (G^{i}_{N} + G^{m}_{N})]$		-281 ± 111*	-7.2 ± 2.3*	327 ± 111*	8.0 ± 2.3**
Heterosis (units)					
H^{i}_{DMxN}		-20 ± 39	.4 ± .8	48 ± 39	.2 ± .8*
Heterosis (%)	-1.4		1.4	1.8	.4
Maternal effect					
$(G^{m}_{DM} - G^{m}_{N})$		86 ± 97	1.7 ± 2.0	-77 ± 97	-1.5 ± 2.0
Direct effect					
$(G^{i}_{DM} - G^{i}_{N})$		-367 ± 148*	-8.9 ± 3.1*	404 ± 147*	9.5 ± 3.1*

[a]DM = Double muscled, N = Normal; sire breed group listed first.

*,**Significant at P<.05 and P<.01, respectively.

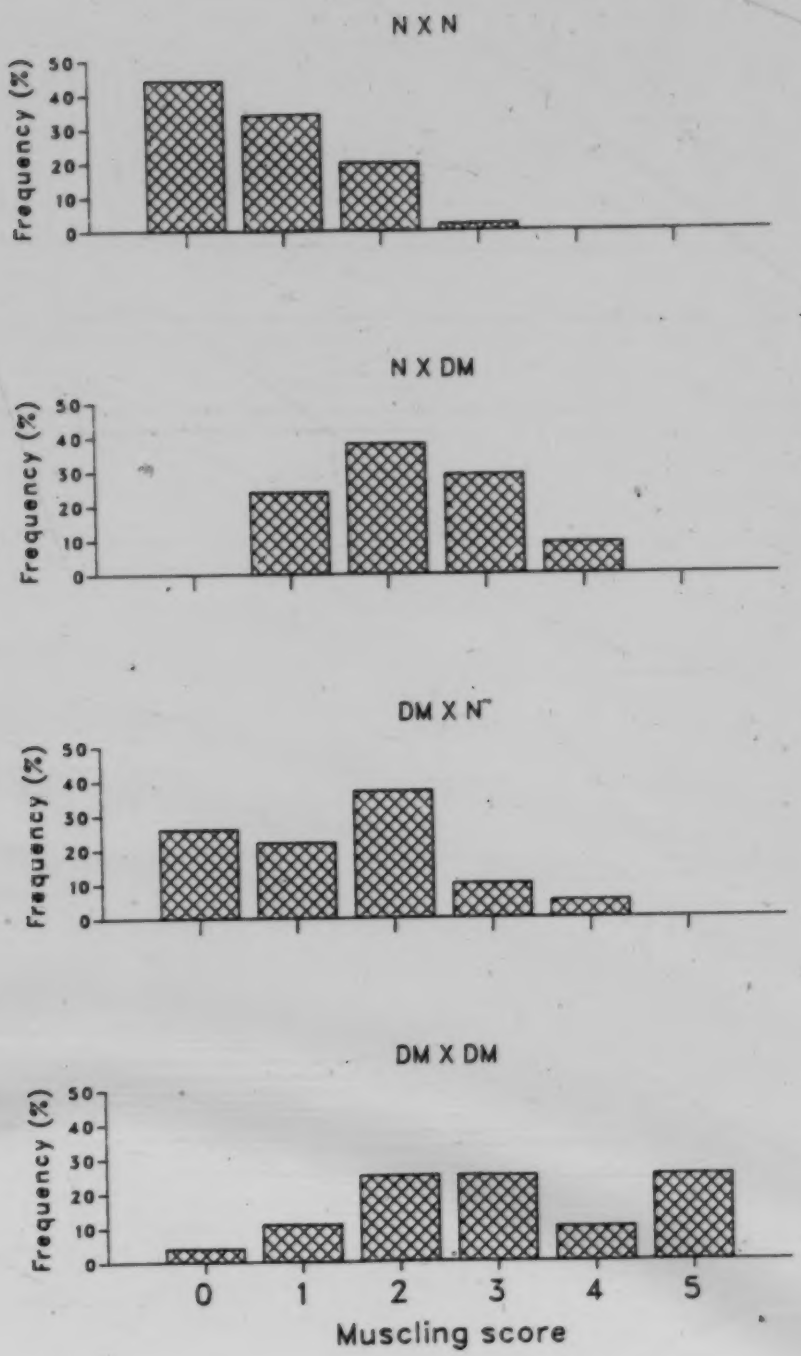
TABLE IV.8. ESTIMATES OF MATING TYPE MEANS, HETEROSIS, MATERNAL AND DIRECT EFFECTS FOR RIB JOINT DISSECTION TRAITS (RIB JOINT WEIGHT CONSTANT BASIS: II)

Item[a]	No.	Bone		Muscle:fat	Muscle:bone
		Wt, g	%		
Mating type means					
DM x DM	16	690 ± 19	14.7 ± .4	3.3 ± .3	4.2 ± .2
N x N	40	735 ± 10	15.4 ± .2	1.8 ± .2	3.4 ± .1
DM x N	59	689 ± 9	14.5 ± .2	2.2 ± .2	4.0 ± .1
N x DM	20	684 ± 17	14.5 ± .4	2.2 ± .3	3.9 ± .1
Straightbred differences					
$[(G^{i}_{DM} + G^{m}_{DM}) - (G^{i}_{N} + G^{m}_{N})]$		-45 ± 18	-.7 ± .3	1.5 ± .3**	.8 ± .1**
Heterosis (units)					
H^{i}_{DMxN}		-52 ± 24	-1.1 ± .5	-.4 ± .2	.2 ± .1
Heterosis (%)		-7	-7.3	-15.7	5.3
Maternal effect					
$(G^{m}_{DM} - G^{m}_{N})$		-5 ± 16	.0 ± .3	.0 ± .3	-.1 ± .1
Direct effect					
$(G^{i}_{DM} - G^{i}_{N})$		-40 ± 25	-.7 ± .4	1.5 ± .4*	.9 ± .2**

[a]DM = Double muscled, N = Normal; sire breed group listed first.

*,**Significant at $P<.05$ and $P<.01$, respectively.

Figure IV.1. Distribution of muscling scores at one year of age among the male progeny of the four mating types.
(0 - normal muscling, 5 - extremely heavy muscling).


N X N
Frequency (%)
50
40
30
20
10
0
N X DM
Frequency (%)
50
40
30
20
10
0
DM X N
Frequency (%)
50
40
30
20
10
0
DM X DM
Frequency (%)
50
40
30
20
10
0
0
1
2
3
4
5
Muscling score

E. LITERATURE CITED

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V. CARCASS CHARACTERISTICS OF YEARLING NORMAL AND DOUBLE MUSCLE CROSS BULLS[1]

A. INTRODUCTION

Double muscling in cattle is believed to be under the control of a single autosomal gene with modifier genes affecting its phenotypic expression (Nott and Rollins, 1979; Menissier, 1982b; Hanset and Michaux, 1985). The double muscle (DM) syndrome is characterized by a generalized hypertrophy of muscles, a reduction in adipose tissue and a reduction in weight of the skeleton (Vissac, 1968; Shahin and Berg, 1985a). DM cattle, therefore, tend to have a higher dressing percentage, less inter- and intra-muscular fat and a higher muscle:bone ratio than normal (N) cattle. Shahin and Berg (1985b) have shown that muscles most affected by the syndrome are the 'high priced' muscles. DM cattle are, however, reported to show some degree of subfertility, higher incidences of dystocia and calf mortality and increased stress susceptibility compared to normal cattle (Menissier, 1982a; Arthur et al., 1988).

While cattle showing the DM syndrome are used in commercial beef production systems in Europe, their deliberate use in North America has been limited to a few research herds. However, interest in the use of DM bulls in breeding programs has increased recently in North America and several prominent bull studs have DM semen available commercially. The feasibility of such breeding programs have been reported by Rollins et al. (1980) and Arthur et al. (1989a,b). In

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[1]A version of this chapter is in press. Arthur, P.F., M. Makarechian, M.A. Price and R.T. Berg. 1989. Can. J. Anim. Sci. Vol. 69 No.4.

Canada, a higher price is often paid steer carcasses relative to heifer carcasses even at constant fatness (grades), partly in recognition of the greater lean yield of the former carcasses (Jones et al., 1987). For breeding programs involving DM cattle to be economically feasible, the higher lean yield of DM cross (DMx) carcasses should be reflected in the price paid for such carcasses. The objectives of this study, therefore, were (1) to compare the carcass characteristics of yearling DMx and N bulls, and (2) to ascertain if there is a superiority in lean yield for DMx carcasses within either A1 or A2 Canadian carcass grade classes.

B. MATERIALS AND METHODS

Animals and Management

Cattle showing the DM syndrome have been maintained at the University of Alberta ranch at Kinsella since 1967. It is a synthetic (composite) breed group, with the average breed composition of the breeding herd at the beginning of this study being approximately 47 percent Angus, 14 percent each of Charolais, Galloway and Hereford, and 11 percent other breeds. The normal (N) cattle was a group of crossbred cattle with no evidence of the DM condition with at least 50 percent Hereford breeding and the remaining percentage made up of Angus, Charolais and Galloway. Reciprocal crossings between DM and N cattle were made over three breeding seasons starting in the summer of 1983. Fifty-nine DM x N (DMx) and forty N x N (N) yearling bulls born over three calving seasons were used in this study. Details on the feeding and management of these animals have been reported by Arthur

et al. (1989a).

Slaughter and Carcass Evaluation

Bulls approaching slaughter condition were measured ultrasonically[2], at weekly intervals, for backfat thickness between the 12th and 13th ribs at the right side. Bulls with an estimated backfat thickness corresponding to the midpoint between the Canada A1 and A2 carcass grades (6 - 8 mm) were shipped for slaughter a week later. Bulls were fasted for 24 hour, then trucked 150 km to a commercial packing plant in Edmonton, where they were weighed and slaughtered within a few hours of arrival. Carcasses were chilled (1-3°C) overnight after which carcass length was measured according to the method described by Yeates (1952). Agriculture Canada graders provided a grade and an appraisal for each carcass. The appraisal used was the standard ML 107 (blue tag) appraisal devised for Record of Performance testing, which consisted of a number of measurements including warm carcass weight, grade, meat color, marbling score (range 1 to 10, higher numbers mean less visible marbling), area of longissimus muscle (*m. longissimus thoracis*; "rib eye area") and fat cover at three positions over the longissimus muscle at the quartering (12-13th ribs) position. A few carcasses which were graded B1 in 1985 (first year of study) as a result of dark meat but which had fat thicknesses greater than 4 mm were reclassified as B2 to reflect the grading system which came into effect in 1986 (Appendix V.1).

A 10-11-12th rib joint was removed from the right side of each

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[2]Scanogram Model 722, Ithaco, Ithaca, New York, USA.

carcass, trimmed according to the method described by Hankins and Howe (1946), and separated into fat, muscle and bone. The weight of each component was expressed as a percentage of the weight of the rib joint.

Statistical Analysis

Two sets of analyses were performed. The first set involved the whole data set, while the second involved data from either A1 or A2 carcasses only. In the first set of analysis, the data were analyzed on an age constant basis, using age at slaughter as a covariate. The mean age at slaughter to which all data were adjusted was 395.7 days. The data were also analyzed on either a weight constant basis, using either warm carcass weight (for carcass measurements) or rib joint weight (for rib joint measurements) as covariate or on grade fat constant basis using grade fat as a covariate. The mean carcass and rib joint weights to which the data were adjusted were 304.7 kg and 4871.4 g, respectively. The mean grade fat thickness to which all the data were adjusted was 10.0 mm.

In the second set of analysis, data on A1 and A2 carcasses were analyzed separately. For each grade the data were analyzed first with no covariate, then with grade fat thickness as a covariate. The mean grade fat thickness to which the data were adjusted were 7.5 mm and 12.9 mm for A1 and A2 carcasses, respectively.

The data were analyzed by least squares procedures (Harvey 1985) using a fixed model with group (DMx or N) and year as main effects plus the interaction between the two effects. Ratio and percentage data were analyzed without transformation since preliminary

examination of residual plots indicated that data transformation was not required.

C. RESULTS AND DISCUSSION

At a constant age at slaughter (395.7 days), differences between DMx and normal carcasses for slaughter weight, warm carcass weight, carcass length, dressing percentage and marbling score were not significant (P>.05; Table V.1). DMx carcasses had larger (P<.005) rib eye areas and cutability, but had smaller (P<.001) grade fat and average fat thicknesses compared to normal carcasses. Similar results were obtained when the data were adjusted to a constant carcass weight (304.7 kg) (Table V.1).

Muscle:fat and muscle:bone ratios, and percent muscle in the 10-11-12th rib joint were higher (P<.001) in DMx compared to normal carcasses, when the data were adjusted to either a constant grade fat thickness (10.0 mm) or a constant rib joint weight (4871.4 g) (Table V.2). Percent fat and percent bone in the rib joint were lower (P<.005) in DMx compared to normal carcasses. The similarity in the results obtained when the data were evaluated at either age constant, weight constant or grade fat constant (Tables V.1 and V.2) suggests that there are important genetic differences between the two groups for these carcass traits.

While the superiority of DM over N carcasses in lean yield has been well documented (Dumont, 1982; Shahin and Berg, 1985a), there have been few published reports on the lean yield of the progeny from crossing DM and normal cattle, especially under a North American

management system. The results obtained in this study clearly indicate that lean yield, as reflected in the percent muscle in the rib joint, of DMx carcasses is higher than that of normal carcasses. This finding is similar to the results obtained by Rollins et al. (1980) in the United States.

The distribution of carcass grades for DMx and normal carcasses is presented in Table V.3. All the carcasses were graded as youthful (Maturity I, potential Canada A grade). While there is concern that DM animals may not fatten adequately to make the Canada A carcass grade, all the DMx carcasses had sufficient fat, except for one (2 percent) carcass which had less than 4 mm of backfat (B1 grade). A higher percentage (24 vs 15 %) of dark meat was observed among DMx than among N carcasses ($P>.05$). However, further studies are recommended to specifically address the incidence of dark carcasses among DMx animals.

Under the Canadian grading system, carcasses of the same grade can vary in backfat thickness (grade fat) by up to 5 mm. Carcass data for each grade were, therefore, first analyzed with no covariate and then with grade fat thickness as a covariate, to obtain uniformity of carcass fat thickness within grade. Within the A1 carcass grade, rib joints from DMx carcasses had higher ($P<.01$) muscle:fat and muscle:bone ratios and percent muscle and lower ($P<.002$) percent fat than those from normal carcasses (Table V.4). When the data were adjusted to a common grade fat (7.5 mm), similar results were obtained, with rib joints from DMx carcasses having 8.8 percent more ($P<.003$) muscle and 12.2 percent less ($P<.015$) fat than rib joints from normal carcasses. The results obtained for A2 carcasses (Table

V.5) were similar to those obtained for A1 carcasses, except that the magnitude of the differences between DMx and normal carcasses for each of these traits was different for A1 compared to A2 carcasses as illustrated in Figure V.1. At a constant grade fat, while the percentage difference in percent muscle between DMx and normal carcasses for A1 carcass grade was 8.8 ($P<.003$), it was 5.7 ($P<.023$) for A2 carcass grade. It therefore appears that the magnitude of the advantage of DMx over normal carcasses in percent muscle is not the same across carcass grades, and that it seems to decrease with increase in fat thickness. This pattern has also been observed with regards to the advantage in percent muscle of steers over heifers in normal carcasses (Fredeen et al., 1981; Jones et al., 1987). This implies that if a premium price is to be paid for DMx carcasses, different rates should apply for different grades.

The current grading system in Canada is not designed to recognize carcasses within the same grade with superior lean yield. Heifer carcasses, however, are often discounted in price compared to steer or bull carcasses of the same grade. The difference between steer and heifer carcasses in lean content has been found to be about 2 percent for A1 carcasses and almost non-existent for A2 carcasses (Jones et al., 1987). DMx carcasses have significantly higher lean content (percent muscle) than normal carcasses grading either A1 or A2 and hence should command differential pricing.

Although the results obtained in this study were based on rib joint dissections, these rib joint dissections are reasonable estimates of actual carcass composition (Hankins and Howe, 1946; Lunt et al., 1985). The degree of hypertrophy of muscles in DM animals is

not uniform throughout the body (Vissac, 1968; Hanset and Ansay, 1972). Shahin and Berg (1985b), working with cattle from the same herd as used in this study, reported that muscles associated with the 10-11-12th rib joint were only moderately hypertrophied, hence they might be considered a good representative of the whole carcass in animals showing the DM syndrome.

There was significant ($P<.05$) year effect for some of the traits, however, no significant group by year interaction was obtained for any of the traits studied.

The results of this study indicate that DMx carcasses have higher lean yield than normal carcasses. The magnitude of the difference, however, differs across carcass grades, with the difference diminishing with increase in carcass fatness. With the increasing demand for leaner carcasses, it is probable that in the future, DMx carcasses will command a premium price as a reflection of their higher lean yield compared to N carcasses.

TABLE V.1. LEAST SQUARES MEANS AND STANDARD ERRORS FOR CARCASS CHARACTERISTICS OF DOUBLE MUSCLE CROSS (DMx) AND NORMAL BULLS

	Age Constant Basis[a]			Weight Constant Basis[b]		
	DMx	Normal	P[c]	DMx	Normal	P[c]
No. of bulls	59	40		59	40	
Age at slaughter (d)				398.0 ± 2.2	395.1 ± 2.3	.398
Slaughter wt. (kg)	498.2 ± 7.0	516.9 ± 7.8	.078	504.1 ± 2.7	510.4 ± 3.0	.124
Warm carcass wt. (kg)	300.6 ± 4.3	309.1 ± 4.7	.187			
Carcass length (cm)	118.9 ± .7	120.7 ± .8	.092	119.3 ± .5	120.2 ± .6	.266
Dressing percentage	60.4 ± .3	59.8 ± .4	.237	60.6 ± .3	59.7 ± .4	.111
Rib eye area (cm^2)	92.1 ± 1.5	84.9 ± 1.7	.002	93.1 ± 1.3	84.1 ± 1.5	.001
Cutability (%)	60.2 ± .2	58.6 ± .3	.001	60.3 ± .2	58.5 ± .3	.001
Grade fat[d] (mm)	9.1 ± .5	11.3 ± .5	.001	8.9 ± .5	11.3 ± .5	.001
Average fat[e] (mm)	10.4 ± .4	12.7 ± .4	.001	10.3 ± .4	12.6 ± .5	.001
Marbling score[f]	7.5 ± .1	7.4 ± .1	.763	7.5 ± .1	7.4 ± .1	.882

[a]Using age at slaughter as covariate (mean of 395.7 d).

[b]Using warm carcass wt. as covariate (mean of 304.7 kg).

[c]Probability of significance.

[d]Measured at the point of minimum fat cover over the 4th quarter of the longissimus muscle, at the quartering position.

[e]Average of three fat thickness measurements taken at three positions over the longissimus muscle, at the quartering position.

[f]1, most marbled; 9, least marbled.

TABLE V.2. LEAST SQUARES MEANS AND STANDARD ERRORS FOR DISSECTED COMPONENTS OF 10-11-12TH RIB JOINT OF DOUBLE MUSCLE CROSS (DMx) AND NORMAL BULL CARCASSES

	Grade Fat Constant Basis[a]			Weight Constant Basis[b]		
	DMx	Normal	P[c]	DMx	Normal	P[c]
No. of bull carcasses	59	40		59	40	
Rib joint wt. (g)	4785.1 ± 87.5	4884.0 ± 97.7	.466			
Dissected fat wt. (g)	1395.7 ± 34.7	1520.8 ± 38.8	.022	1372.7 ± 31.6	1577.4 ± 34.9	.001
Dissected muscle wt. (g)	2709.7 ± 56.1	2608.8 ± 62.7	.247	2802.8 ± 31.4	2548.0 ± 34.6	.001
Dissected bone wt. (g)	676.0 ± 14.1	749.9 ± 15.7	.001	692.6 ± 9.4	741.0 ± 10.3	.001
Muscle:fat	2.1 ± .1	1.8 ± .1	.001	2.2 ± .1	1.7 ± .1	.001
Muscle:bone	4.0 ± .1	3.5 ± .1	.001	4.1 ± .1	3.5 ± .1	.001
Percent fat	28.8 ± .4	30.7 ± .5	.006	27.8 ± .6	32.0 ± .7	.001
Percent muscle	56.8 ± .5	53.7 ± .5	.001	57.8 ± .6	52.5 ± .7	.001
Percent bone	14.3 ± .2	15.5 ± .2	.001	14.4 ± .2	15.4 ± .2	.001

[a]Using grade fat thickness as covariate (mean of 10.0 mm).

[b]Using rib joint wt. as covariate (mean of 4871.4 g).

[c]Probability of significance.

TABLE V.3. DISTRIBUTION OF CARCASS GRADES FROM DOUBLE MUSCLE CROSS (DMx) AND NORMAL BULL CARCASSES

Carcass Grade[a]	DMx		Normal	
	No.	Percentage	No.	Percentage
A1	28	47	12	30
A2	14	24	18	45
A3	2	3	4	10
B1	1	2		
B2	14	24	6	15

[a]See Appendix V.1.

TABLE V.4. LEAST SQUARES MEANS AND STANDARD ERRORS FOR DISSECTED COMPONENTS OF 10-11-12TH RIB JOINT OF DOUBLE MUSCLE CROSS (DMx) AND NORMAL A1 BULL CARCASSES

	No Covariate				With Covariate[a]			
	DMx	Normal	P[b]	Percentage Difference[c]	DMx	Normal	P[b]	Percentage Difference[c]
No. of carcasses	28	12			28	12		
Muscle:fat	2.4 ± .1	1.8 ± .1	.008	33.3	2.4 ± .1	2.0 ± .2	.061	20.0
Muscle:bone	4.1 ± .1	3.4 ± .2	.009	20.6	4.1 ± .1	3.5 ± .2	.024	17.1
Percent fat	25.7 ± .8	30.8 ± 1.2	.002	-16.6	25.8 ± .7	29.4 ± 1.2	.015	-12.2
Percent muscle	59.5 ± .8	53.2 ± 1.3	.001	11.8	59.4 ± .8	54.6 ± 1.2	.003	8.8
Percent bone	14.7 ± .4	15.9 ± .6	.138	-8.2	14.7 ± .4	15.9 ± .7	.145	-7.6

[a]Using grade fat as covariate; mean of 7.5 mm.

[b]Probability of significance.

[c][(DMx - Normal)/Normal] x 100.

TABLE V.5. LEAST SQUARES MEANS AND STANDARD ERRORS FOR DISSECTED COMPONENTS OF 10-11-12TH RIB JOINT OF DOUBLE MUSCLE CROSS (DMx) AND NORMAL A2 BULL CARCASSES

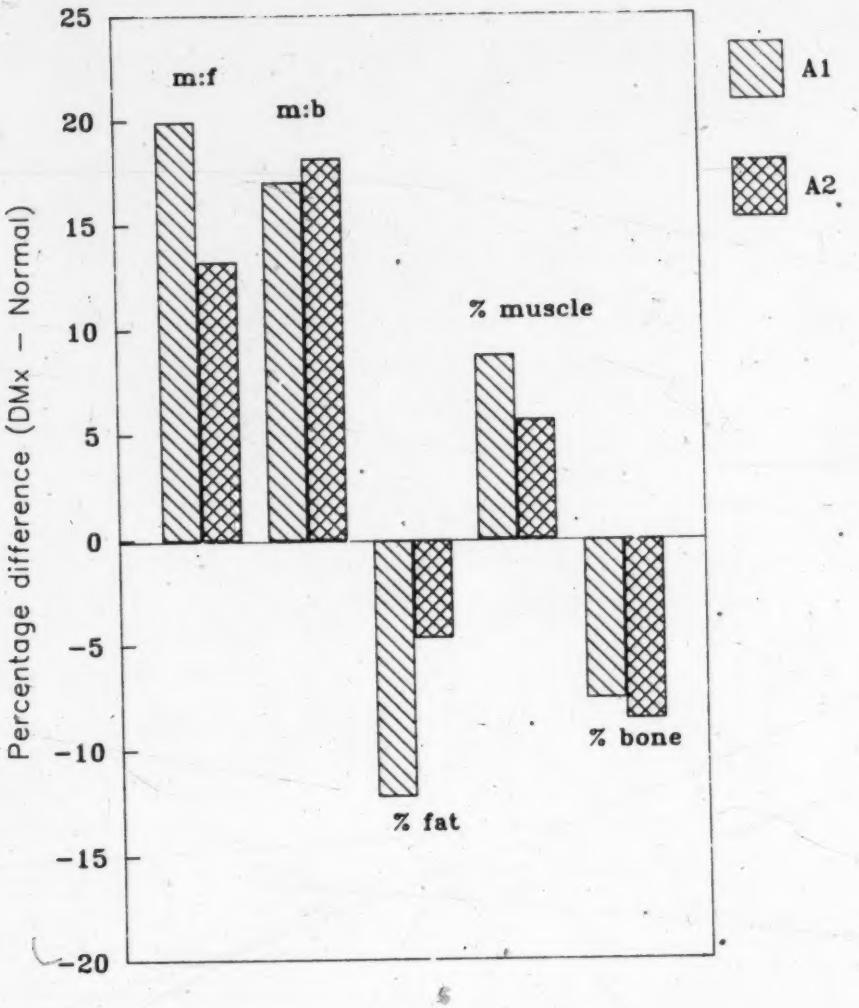
	No Covariate				With Covariate[a]			
	DMx	Normal	P[b]	Percentage Difference[c]	DMx	Normal	P[b]	Percentage Difference[c]
No. of carcasses	14	18			14	18		
Muscle:fat	1.7 ± .1	1.6 ± .1	.262	6.3	1.7 ± .1	1.5 ± .1	.087	13.3
Muscle:bone	4.0 ± .2	3.4 ± .1	.008	17.6	3.9 ± .2	3.3 ± .1	.005	18.2
Percent fat	31.9 ± 1.2	33.2 ± .9	.394	-3.9	32.6 ± 1.0	34.2 ± .7	.145	-4.7
Percent muscle	54.1 ± 1.3	51.5 ± .9	.104	5.1	53.5 ± 1.0	50.6 ± .8	.023	5.7
Percent bone	14.0 ± .4	15.3 ± .3	.005	-8.5	13.9 ± .4	15.2 ± .3	.007	-8.6

[a]Using grade fat as covariate; mean of 12.9 mm.

[b]Probability of significance.

[c][(DMx - Normal)/Normal] x 100.

Figure V.1. Percentage difference in rib joint components between DMx and normal A1 and A2 carcasses.


25
20
15
10
5
0
−5
−10
−15
−20
Percentage difference (DMx − Normal)
m:f
m:b
% muscle
% fat
% bone
A1
A2

D. LITERATURE CITED

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VI. A MOLECULAR GENETICS STUDY OF MUSCLE GROWTH IN DOUBLE MUSCLED CATTLE

A. INTRODUCTION

Recombinant DNA technology offers the potential for rapid genetic improvement in livestock breeding. As a result of this technology specific genes can be manipulated to obtain accelerated genetic improvement. The long term goal of such technology is its eventual application to practical livestock improvement. Beef cattle breeding programs in recent years have been geared towards the efficient production of lean beef. In an attempt to extend the application of recombinant DNA technology from experimental animals, such as mice, to livestock, the double muscled (DM) animal becomes an ideal model for such studies in muscle growth.

Double muscling or muscular hypertrophy is an inherited condition in cattle. DM cattle are known to excel in carcass characteristics due to their increased musculature and limited subcutaneous and intermuscular fat (Butterfield, 1966; Shahin and Berg,1985). Compared to normal cattle, DM cattle have less bone, less fat, more muscle, a higher muscle to bone ratio (Dumont, 1982) and a higher proportion of 'expensive' cuts of meat. Unfortunately, this is accompanied by a number of undesireable traits (low fertility, low calf viability and high stress susceptibility) which make them unacceptable to beef producers despite their superior carcasses.

While there is a strong circumstantial evidence that the DM syndrome is controlled by a single autosomal gene (though modifier genes at other loci are involved), the gene concerned has not been

identified.

The role of hormones in growth and development is well documented (Spencer, 1985). Growth hormone is an anabolic agent which promotes skeletal growth and protein synthesis (Machlin, 1976). Growth hormone action is presently believed to be through other growth factors such as insulin-like growth factor - I (IGF-I) and IGF-II (Daughaday et al., 1972). Other hormones such as insulin, testosterone and thyroid hormones are also known to influence growth (Spencer, 1985). These hormones related to growth and development, are therefore, good starting points for research into growth related genes at the molecular level. A prototype experiment conducted by Salmon et al. (1988), using restriction site analysis, revealed that the growth hormone allele in a line of mice selected for high body weight was structurally different from the control growth hormone allele.

The objective of this study, therefore, was to characterize allelic forms of growth hormone and IGF-II genes, among DM and normal cattle using restriction site analysis.

B. MATERIALS AND METHODS

DM cattle have been maintained as a separate breed group at the University of Alberta ranch at Kinsella since 1967. It is a composite breed group with average breed composition of approximately 47 percent Angus, 14 percent each of Charolais, Galloway and Hereford, and 11 percent from other breeds. DM calves born during the 1987 calving season as a result of mating DM bulls and cows were scored visually for muscling on a scale of zero to five, with zero indicating normal

muscling and five representing extreme muscular hypertrophy. Six of these bull calves which showed extreme muscular hypertrophy (muscling score of 4 or 5) were selected. Four older bulls with muscling scores of 4 or 5 were added to make up the DM group used in this study. For comparison, ten bulls with normal muscling from another composite breed group, Beef Synthetic (SY), with average breed composition of Angus (37%), Charolais (33%), Galloway (21%) and other breeds (9%), selected at random were used.

Approximately 20 ml of blood was taken from each animal by venipuncture of the jugular vein into vacutainers containing EDTA (ethylene-diaminetetraacetate). The blood samples were chilled immediately and stored at 0° - 4°C until DNA extraction. DNA samples, containing 10 μg of DNA, were digested with eight commercially obtained[1] restriction endonucleases (Table VI. 1) and electrophoresed on .7% agarose gels. The restricted DNAs were then transferred to a hybridization transfer membrane (GeneScreenPlus[2]).

Two cDNA probes, radioactively labelled, were used for hybridization. The cDNA probes were bovine growth hormone (Woychik et al., 1982) and IGF-II (Bell et al., 1985). The procedures for DNA extraction, DNA digestion and electrophoresis, probe labelling and hybridization were described by Bork et al. (1989) (Appendix VI.1).

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[1]Bethesda Research Laboratories, Burlington, Ontario; Pharmacia, Dorval, Quebec.
[2]New England Nuclear Research Products, Boston, MA.

C. RESULTS AND DISCUSSION

Growth Hormone

Hybridization of the radioactively labelled growth hormone cDNA to the EcoR I digested genomic DNA on the hybridization transfer membrane showed two major bands for both DM and SY (Figure VI.1). These bands corresponded with approximately 4.6 kb and 11 kb fragments. Generally the 11 kb EcoR I band was less intense than the 4.6 kb band. Growth hormone nucleotide sequences have been reported to be contained in an approximately 4.3 kb EcoR I fragment (Woychik et al., 1982; Gordon et al., 1983), which corresponds with the 4.6 kb band obtained in this study. Two bands were obtained by Woychik et al. (1982) and Gordon et al. (1983) on complete EcoR I digestion of genomic DNA. The second band corresponded with a 11 kb fragment in the study by Woychik et al. (1982) and a 8.4 kb fragment in the study by Gordon et al. (1983). In both studies the possibility that the second band represented a partial digestion product was ruled out. Gordon et al. (1983) suggested that this second fragment with sequences related to growth hormone sequences could be a duplicated growth hormone-like gene, such as has been shown to occur in humans (Fiddes et al., 1979; Phillips et al., 1981), or could have resulted from cross hybridization between growth hormone and placental lactogen sequences as has been demonstrated by Fiddes et al. (1979).

Some of the DNA samples showed hybridization bands other than the 11 kb and 4.6 kb EcoRI fragments (Figure VI.1). These bands were significantly less intense and corresponded with 3.5 kb and 5.8 kb fragments. Two of the DM and one of the SY DNA samples had the 3.5 kb

fragment in addition to the 4.6 kb fragment. The 5.8 kb fragment was observed in three DM DNA samples. Allelic polymorphism has been found in bovine growth hormone (Fellows and Rogol, 1969). Allelic forms of the same gene for a DNA sample will usually have similar hybridization band intensity. The 3.5 kb and 5.8 kb fragments obtained in some of the DNA samples cannot be allelic forms of the growth hormone gene since these bands were significantly less intense than the 4.6 kb growth hormone band. The 5.8 kb band could be due to the presence of partial endonuclease digestion products, while the 3.5 kb band could be due to contamination from the plasmid which contained the cDNA probe. Examination of the rate of gain and the degree of muscling of the DM animals whose DNA samples showed an extra band did not show any significant difference from those DM animals possessing only the 4.6 kb fragment.

DNA digested with Pvu II yielded two bands after hybridization with growth hormone cDNA (Figure VI.2). One fragment was approximately 7.1 kb while the other fragment was less than 1 kb. DNA digested with Sau3A yielded only one band which corresponds with a fragment less than 1 kb. DNA digested with Xba I yielded two bands which corresponded approximately with 10.8 kb and 6.9 kb fragments. The results obtained with Xba I digestion are in agreement with those reported by Gordon et al. (1983), with respect to the number of bands and the approximate sizes of these fragments. Digestion with Hinf I yielded fragments less than 1 kb in size (bands not shown). For each of these enzymes, the banding patterns in DM were similar to those in SY DNA.

Due to the fact that there was lack of between group (DM or SY)

variation for each of the endonucleases, it could be concluded that restriction site analysis of the growth hormone gene did not reveal differences between SY and DM cattle for this gene.

Insulin-like Growth Factor-II

After EcoR I digestion of genomic DNA, IGF-II cDNA hybridized to a single band in both DM and SY, corresponding with 4.7 kb fragment (Figure VI.3). Genomic DNA digested with Pst I yielded four bands after hybridization with IGF-II cDNA, corresponding with 6.0 kb, 2.3 kb, 1.7 kb and 1.2 kb fragments (Figure VI.4). While the digestion with Kpn I yielded no bands, that with Hind III yielded two bands upon hybridization with IGF-II cDNA, corresponding with 12.2 kb and 3.5 kb fragments. There are no reports in the literature on the hybridization patterns of IGF-II cDNA to bovine genomic DNA although hybridization to DNA of other species has been reported (Tricoli et al., 1984). The hybridization patterns of IGF-II for DM were similar to those for SY for each of the endonucleases used.

It can therefore be concluded from this study that no differences were obtained between DM and SY cattle for the growth hormone and IGF-II genes using restriction site analysis.

TABLE VI.1. RESTRICTION ENDONUCLEASES USED AND THEIR RECOGNITION SEQUENCES AND CLEAVAGE SITES

Endonuclease	Recognition sequence with cleavage site (↓↑)
EcoR I	5'-G↓AATT C-3' 3'-C TTAA↑G-5'
Hind III	5'-A↓AGCT T-3' 3'-T TCGA↑A-5'
Hinf I	5'-G↓ANT C-3' 3'-C TNA↑G-5'
Kpn I	5'-G GTAC↓C-3' 3'-C↑CATG G-5'
Pst I	5'-C TGCA↓G-3' 3'-G↑ACGT C-3'
Pvu II	5'-CAG↓CTG-3' 3'-GTC↑GAC-5'
Sau3A	5'-↓GATC -3' 3'- CTAG↑-5'
Xba I	5'-T↓CTAGA-3' 3'-A↑GATCT-5'

Figure VI.1. Autoradiogram showing hybridization pattern of growth hormone cDNA to EcoR I digest of genomic DNA from DM and SY cattle. Each lane received 10 μg DNA, corresponding, from left to right, to samples from the following animals; 323-6, 279-6, 520-5, 518-5, 513-6, 510-6, 529-7, 524-7, 517-7, 510-7, 507-7 and 505-7. An undetermined amount of DNA from the 510-6 and 505-7 samples leaked from the electrophoresis gel during loading.

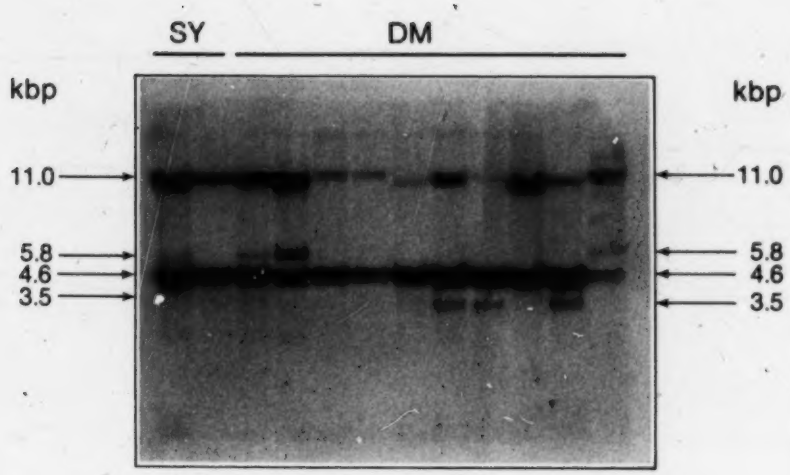

SY
DM
kbp
kbp
11.0
5.8
4.6
3.5
11.0
5.8
4.6
3.5

Figure VI.2. Autoradiogram showing hybridization patterns of growth hormone cDNA to genomic DNA from DM and SY cattle digested with various endonucleases (P, Pvu II; S3, Sau3A; X, Xba I). Bands within the S region corresponded with fragments < 1 kb.

For each endonuclease, each lane received 10 μg DNA, corresponding, from left to right, to samples from the following animals; 279-6, 510-7 and 517-7.

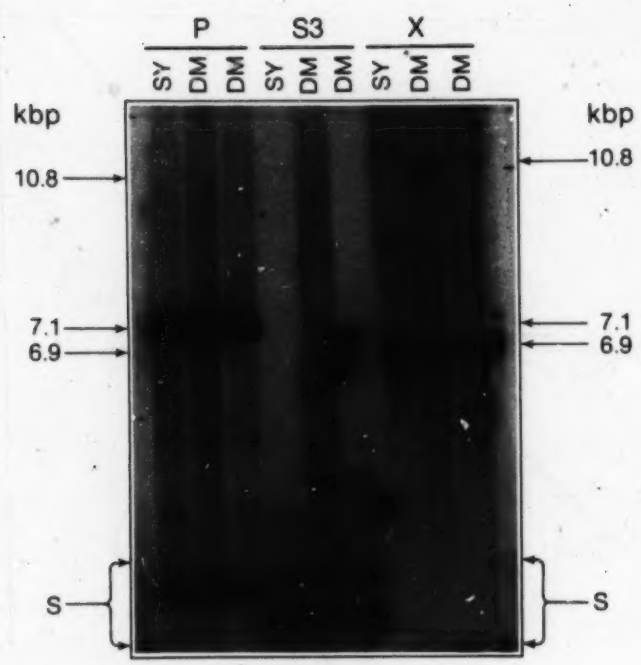

P
S3
X
SY
DM
DM
SY
DM
DM
SY
DM
DM
kbp
kbp
10.8
10.8
7.1
6.9
7.1
6.9
S
S

Figure VI.3. Autoradiogram showing hybridization pattern of IGF-II cDNA to EcoR I digest of genomic DNA from DM and SY cattle.

Each lane received 10 μg DNA, corresponding, from left to right, to samples from the following animals; 323-6, 279-6, 520-5, 518-5, 513-6, 510-6, 529-7, 524-7, 517-7, 510-7, 507-7 and 505-7. An undetermined amount of DNA from the 510-6 and 505-7 samples leaked from the electrophoresis gel during loading.

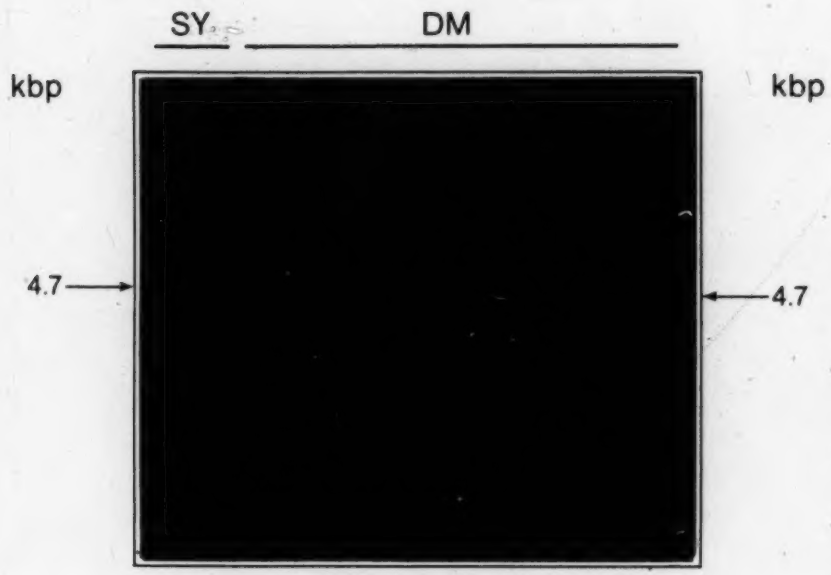
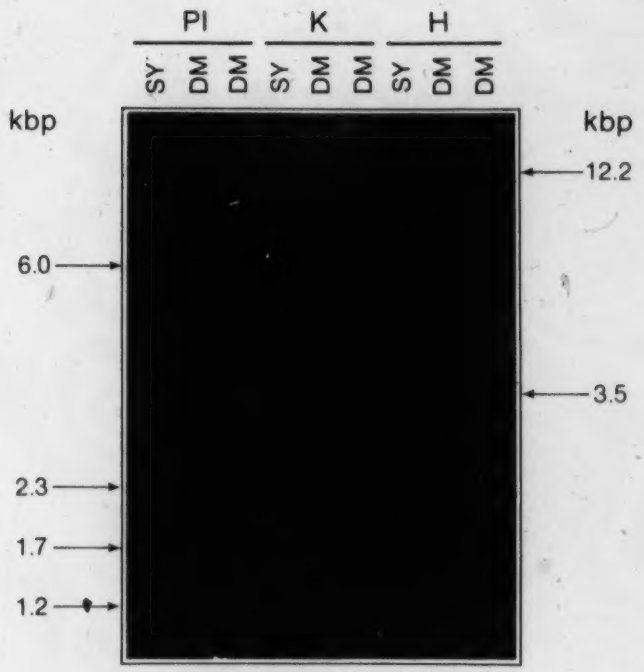

SY
DM
kbp
kbp
4.7
4.7

Figure VI.4. Autoradiogram showing hybridization patterns of IGF-II cDNA to genomic DNA from DM and SY cattle digested with various endonucleases (PI, Pst I; K, Kpn I; H, Hind III).

For each endonuclease, each lane received 10 μg DNA, corresponding, from left to right, to samples from the following animals; 279-6, 517-7 and 505-7.


PI
K
H
SY
DM
DM
SY
DM
DM
SY
DM
DM
kbp
kbp
12.2
6.0
3.5
2.3
1.7
1.2

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VII. PLASMA GROWTH HORMONE AND INSULIN CONCENTRATIONS IN DOUBLE-MUSCLED AND NORMAL BULL CALVES[1]

INTRODUCTION

Double muscling or muscular hypertrophy is an inherited condition in cattle, manifested by a generalized hypertrophy of muscles, a reduction in adipose tissue, and a reduction in weight of the skeleton (Vissac, 1968; Menissier, 1982; Shahin and Berg, 1985). The physiological/biochemical processes responsible for the double-muscled (DM) syndrome are not known. While some researchers speculate that the abnormalities at the cell membrane level may cause these peculiar characteristics (King et al., 1976; Basarab et al., 1980), others suggest that the abnormality may be primarily due to an endocrine imbalance (Pomeroy and Williams, 1962; Vissac et al., 1974).

Growth hormone promotes protein synthesis while insulin promotes synthesis of metabolites (Spencer, 1985). Hence these hormones could be involved in the development of muscular hypertrophy and leaness associated with DM cattle. There have been few reports on the levels of growth hormone and insulin in the DM compared to normal (N) cattle. Michaux et al. (1982) reported higher plasma levels of growth hormone and lower levels of insulin in DM compared to N bulls at certain ages in the first year of life. The objective of this study was to compare the plasma growth hormone and insulin concentrations in DM and N bulls during the first nine months of life, and to relate these to differences in growth rate between the two breed groups.

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[1]A version of this chapter has been accepted for publication. Arthur, P.F., M. Makarechian, R.K. Salmon and M.A. Price. J. Anim. Sci.

MATERIALS AND METHODS

Cattle showing the DM syndrome have been maintained as a separate breed group at the University of Alberta ranch at Kinsella since 1967. It is a composite breed group with average breed composition of approximately 47% Angus, 14% each of Charolais, Galloway and Hereford, and 11% from other breeds. Another composite breed group, Beef Synthetic, with average breed composition of Angus (37%), Charolais (33%), Galloway (21%) and other breeds (9%), was used as the normal (N) group. Nineteen DM and 20 N bull calves born in the spring of 1987 were used in the study. The DM calves were scored visually, at birth, for muscling on a scale of zero to five, with zero indicating normal muscling and five representing extreme muscular hypertrophy. The DM calves used showed various degrees of muscular hypertrophy (muscling scores ranging from 1 to 5) while the normal calves had normal muscling (muscling scores of 0 and 1). Calves remained with their dams on the range until weaning at approximately six months of age with no creep feeding. After weaning calves were placed in feedlot and fed, ad libitum, a high energy diet (Table VII.1). Weights of the calves were recorded at birth and at monthly intervals throughout the experimental period.

A 10 ml blood sample was taken from each animal from the jugular vein by venipuncture into tubes with .5 ml of a solution of .065M EDTA and 1 mg aprotinin[2] (a protease inhibitor) in saline, on 10 different dates corresponding to the mean ages of 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5.5, 6.5 and 9 months. Collection of blood samples was started

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[2]Sigma Chemical Co., St. Louis, Mo.

at 0900 h each sampling date. During the preweaning period calves were separated from their dams 2 h prior to blood sample collection. The samples were chilled immediately after collection, centrifuged within 10 h, and plasma stored at -20°C until analyzed. Each plasma sample was analyzed in duplicate for growth hormone and insulin by radioimmunoassay procedures described by de Boer and Kennelly (1989). The intra- and inter-assay coefficients of variation were 9.7 and 8.8%, respectively, for growth hormone, and 6.7 and 12.2%, respectively, for insulin.

Growth data were analyzed using a completely randomized design (Steel and Torrie, 1980). Hormone concentration data were analyzed using repeated measures procedure (SAS, 1987). The model used included the fixed effects of breed group, age and breed group by age interaction. Animals within breed group were included in the model as random effects, and the mean squares were used as the error term for testing significance of mean differences between breed groups. Residual mean squares were used to test significance of the other effects. Linear and quadratic effects of age were fitted in a regression model (Steel and Torrie, 1980), to determine the nature of the response in the concentration of each hormone to the effect of age. Higher order polynomials were found to be non-significant. The relationships between the growth traits and hormone concentrations were determined by correlation analysis of the particular growth trait with the mean hormone concentration over the 10 sampling dates for each animal; the number of observations for each correlation analysis being equal to the number of animals. Residual correlations were also computed from residual variances and covariances to remove the effect

due to breed group.

RESULTS AND DISCUSSION

DM bull calves were lighter (P<.0001) at birth, and at any particular age throughout the study period than N bull calves (Table VII.2). Both preweaning and postweaning rates of gain were lower (P<.001) in the DM than in N calves. Although some reports indicate that DM cattle have superior growth potential than N cattle, other reports are to the contrary; showing DM cattle as having lower growth rate leading to lighter mature weight. Postweaning growth rate of DM calves has been reported to be slower than that of N calves in most of the British breeds (Nott and Rollins, 1979; Geay et al., 1982; Menissier, 1982). The average breed composition of the DM cattle in this study was 75% British breeds. The differences in sire selection criteria used in the two breed groups, as the Beef Synthetics were selected for growth rate and the DM for muscular hypertrophy, could also have contributed to the difference in growth rate of these two breed groups (Arthur et al., 1989a).

The DM bulls had lower (P<.01) mean growth hormone concentration than N bull calves (Table VII.3). Differences between DM and N bulls in circulating levels of growth hormone occurred prior to the age of 4.5 mo, after which both breed groups had similar growth hormone concentrations (Figure VII.1). Michaux et al. (1981) reported higher levels of plasma growth hormone in DM than in N (conventional) bulls at 2.5 mo but lower levels at 7.5 mo of age, while the levels at 4.5 and 12 mo of age in the two breed types were similar. Michaux et al. (1981) attributed the differences in growth hormone concentration

between DM and N cattle at 2.5 and 7.5 mo of age, to differences in body weight and not to the DM syndrome.

Growth hormone promotes protein synthesis in muscle and linear skeletal growth (Machlin, 1976). It could be speculated that the heavy muscular development in the DM bulls might be the result of higher growth hormone level. However, in the present study the DM calves had lighter weights than N calves (Table VII.2), and in an earlier study (Arthur et al., 1989b) DM yearling bulls had smaller carcass length than N bulls. This indicates that the muscular hypertrophy was not accompanied by higher linear skeletal growth as expected from growth hormone action. The correlation between growth hormone concentration and the degree of muscling (DM score) of the DM calves was not significant (Table VII.4), indicating that factors other than the growth hormone concentration may be responsible for the muscular hypertrophy in the DM bulls. This seems to be compatible with the findings of Lawrie et al. (1964) that changes in weight and total nitrogen concentration of muscles observed in DM cattle are different from those caused by growth hormone and steroid hormone administration. However, the higher mean plasma growth hormone concentration observed in N over DM bulls is consistent with the heavier body weight and higher growth rate in N over DM bulls (Table VII.2). When body weight at 9 mo of age was used as a covariate, no significant differences were obtained between DM and N bulls for mean growth hormone concentration. Correlation coefficients of various body weights and preweaning ADG with mean growth hormone concentrations were significant and positive (Table VII.4). However, residual correlations were low and non-significant, indicating that across

breed groups, differences in growth hormone concentration are related to differences in growth rate, while within breed group (after removing the effect of breed group), growth hormone concentration was not directly related to growth rate. These results are in agreement with the higher growth hormone concentrations obtained in steers with high versus low growth potentials (Ohlson et al., 1987; Verde and Trenkle, 1987). The results are also in agreement with reports of higher growth hormone concentration in larger Simmental compared with the smaller Hereford bulls (Ohlson et al., 1981).

The nature of the response in growth hormone concentration to the effect of age was linear ($P<.05$). Between the ages of 1.5 and 4.5 mo, however, mean growth hormone concentrations fluctuated in both breed groups, but stabilized at about 28 ng/ml after 5.5 mo of age until the end of the study (Figure VII.1). Growth hormone does not appear to be important in growth regulation during fetal life and the newborn appears to have an immature endocrine system early in life (Dauzier, 1980). The fluctuations in growth hormone concentration obtained before 4.5 mo of age could be due to the immaturity of the endocrine system at that stage and the consequent lack of adequate feedback regulation of growth hormone secretion (Turner and Munday, 1976; Gluckman, 1985).

A general decrease in growth hormone concentration with age has been observed in steers (Trenkle, 1977; Beeby and Swan, 1983; Verde and Trenkle, 1987). In bulls, however, a rise in growth hormone concentration at approximately 6 to 8 months of age has been reported (Joakimsen and Blom, 1976; Keller et al., 1979; Michaux et al., 1981). The rise in growth hormone concentration to about 28 ng/ml in both

breed groups at around 5.5 mo of age is consistent with these findings in bulls. It has been suggested that modifications in the endocrine system during the onset of puberty and its consequent increase in testosterone secretion could interact with growth hormone secretion (Ronge and Blum, 1989).

The mean plasma insulin concentration in DM bulls was lower ($P<.01$) than that in N bulls (Table VII.3). The plasma insulin concentrations in DM bulls were lower than in N bulls at all ages studied except at 2.5 months of age (Figure VII.1). Michaux et al. (1982) also reported lower plasma insulin concentrations and corresponding leaner carcass in DM relative to N bulls.

Insulin is involved in lipid metabolism by promoting lipogenesis and inhibiting lipolysis (Brockman, 1978). Carcass characteristics studies with bulls from the same herds as used in this study, indicated that DM bull carcasses had less fat compared to N bull carcasses (Shahin and Berg, 1985; Arthur et al., 1989b). This is consistent with the lower levels of insulin obtained in DM relative to N bulls. Insulin concentration was positively correlated with body weight (Table VII.4). This was probably because the leaner DM bulls were smaller than the relatively fatter but larger N bulls. Residual correlation coefficients between the growth traits and insulin concentration were low and non-significant.

The nature of the response in insulin concentration to the effect of age was described by linear and quadratic effects ($P<.0001$) of age (Figure VII.1). Insulin levels remained generally constant from 1.5 to 6.5 mo of age in both breed groups at around .75 ng/ml but rose sharply thereafter to about 1.67 ng/ml by 9 mo of age. Insulin

concentration has been observed to rise with increase in the length of the postweaning feeding period (Trenkle and Topel, 1978; Eversole et al., 1981; Beeby and Swan, 1983; Verde and Trenkle, 1987). Although the rise in insulin concentration observed after 6.5 mo of age was sharper than those reported by the other researchers, it coincided with the time when the bulls were started on a high energy diet in the feedlot after they were weaned at 6 mo of age.

The mean molar ratio of insulin to growth hormone was higher ($P<.05$) for DM than N bull calves (Table VII.3). DM bulls had a higher mean value for this ratio than N bulls at 1.5 mo of age, however, by 9 mo of age the pattern had been reversed with N bulls having a higher mean value than DM bulls (Figure VII.1). Insulin and growth hormone appear to function counter to the other and the ratio of the concentrations of the two hormones is important in energy metabolism (Rabinowitz et al., 1966). Hart et al. (1979), indicated that a decrease in this ratio would increase fat mobilization. Accretion of fat in beef cattle occurs to a higher degree during the postweaning rather than the preweaning period. During postweaning, DM bulls had lower insulin:growth hormone ratio, indicating that in the DM, compared to the N bulls, the level of growth hormone relative to that of insulin might have been metabolically significant to limit the partitioning of energy to adipose tissue, resulting in leaner DM carcasses.

Growth hormone and insulin secretion is episodic in cattle (Anfinson et al., 1975) and hence to establish secretory profile of each animal frequent sampling (every 15 min) over a time span of approximately 24 h has commonly been used. While this sampling

procedure allows the characterization and comparison of temporal secretory patterns, the labor intensive nature of such experiments have generally limited both the number of animals studied as well as the number of sampling dates. The single sample procedure employed in this study was found to be more practicable for the initial characterization of the pre- and postweaning growth hormone and insulin levels of each breed group and age. Therefore, the hormone concentration for each individual animal at a particular sampling date, in this study, might not be representative of the individual's hormonal status at the time. However, by using a larger number of animals for each breed group, in this study, it was expected that the mean hormone concentration of all the bulls in a breed group and/or at a particular age is representative of the breed group or the particular age. The distributions of hormone concentrations at various ages (Figure VII.2) showed that a few samples had higher concentrations of growth hormone and insulin which may correspond to secretory spikes. This is indicated by the general skewness of the distributions towards the lower concentrations with a few higher concentrations for both breed groups at the different ages.

It can be concluded from this study that differences in the concentration of growth hormone between DM and N bulls were related to differences in growth rate and weight of the bulls from these two breed groups rather than to the degree of muscling. Differences in the concentrations of insulin were related to the differences in the degree of fatness of the bulls in these two breed groups.

TABLE VII.1. COMPOSITION OF GRAIN MIXTURE

Ingredients	Air dry composition
Barley, %	63
Oats, %	22
Alfalfa pellets, %	10
Canola meal, %	5
Total, %	100
Chemical Analysis	*Per kg dry matter*
Dry matter, %	90.0
Digestible energy, MJ	14.2
Metabolizable energy, MJ	11.8
Protein, g	133.9
Acid detergent fibre, g	122.0
Calcium, g	5.7
Phosphorus, g	4.7
Salt, g	1.6

TABLE VII.2. LEAST SQUARES MEANS OF GROWTH TRAITS OF DOUBLE-MUSCLED (DM) AND NORMAL (N) BULL CALVES

Item	DM	N	SE	P
No. of calves	19	20		
Birth wt., kg	33.0	43.9	1.5	.0001
1.5 month wt., kg	71.4	95.9	3.1	.0001
6 month wt., kg[a]	198.1	263.0	7.1	.0001
9 month wt., kg	318.4	408.0	10.5	.0001
Preweaning ADG, kg/day	.94	1.23	.03	.0001
Postweaning ADG, kg/day	1.31	1.59	.04	.001

[a]Weaning weight.

TABLE VII.3. LEAST SQUARES MEANS OF PLASMA GROWTH HORMONE AND INSULIN CONCENTRATIONS AND MOLAR RATIO OF THE HORMONES FOR DOUBLE-MUSCLED (DM) AND NORMAL (N) BULL CALVES

Item	DM	N	SE	*P*
No. of calves	19	20		
Growth hormone, ng/ml	20.01	24.70	4.89	.01
Insulin, ng/ml	.80	.91	.15	.01
Molar ratio insulin:growth hormone	.27	.21	.11	.05

TABLE VII.4. COEFFICIENTS OF CORRELATIONS BETWEEN GROWTH TRAITS AND MEAN[a] PLASMA GROWTH HORMONE AND INSULIN CONCENTRATIONS OF COMBINED GROUPS OF DOUBLE-MUSCLED (DM) AND NORMAL (N) BULL CALVES

	Growth hormone		Insulin	
Item	r	*P*	r	*P*
1.5 mo wt.	.22	.09	.25	.06
3 mo wt.	.24	.08	.33	.02
4 mo wt.	.31	.03	.25	.06
6 mo wt.	.32	.03	.36	.01
7 mo wt.	.33	.02	.29	.04
8 mo wt.	.31	.03	.28	.05
9 mo wt.	.31	.03	.29	.04
Preweaning ADG	.31	.03	.39	.01
Postweaning ADG	.16	.18	.15	.19
DM score[b]	-.19	.22	.05	.42

[a]The mean of 10 concentrations corresponding to the 10 sampling dates for each animal; no. of observations = no. of animals = 39.

[b]Only DM data used.

Figure VII.1. Changes in plasma concentrations of growth hormone (GH) and insulin and molar ratio of the two hormones, with age in double-muscled (DM) and normal (N) bull calves.

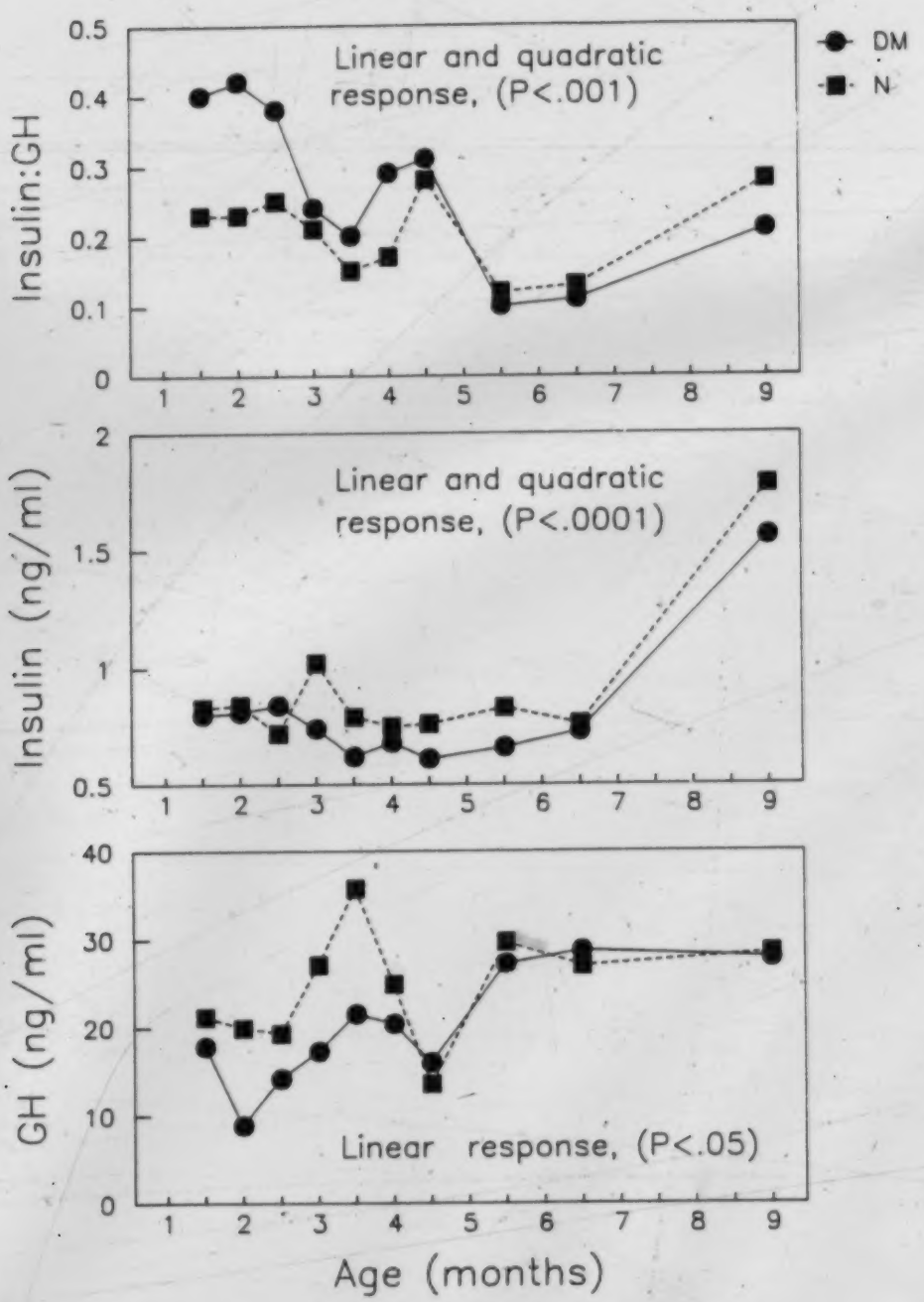
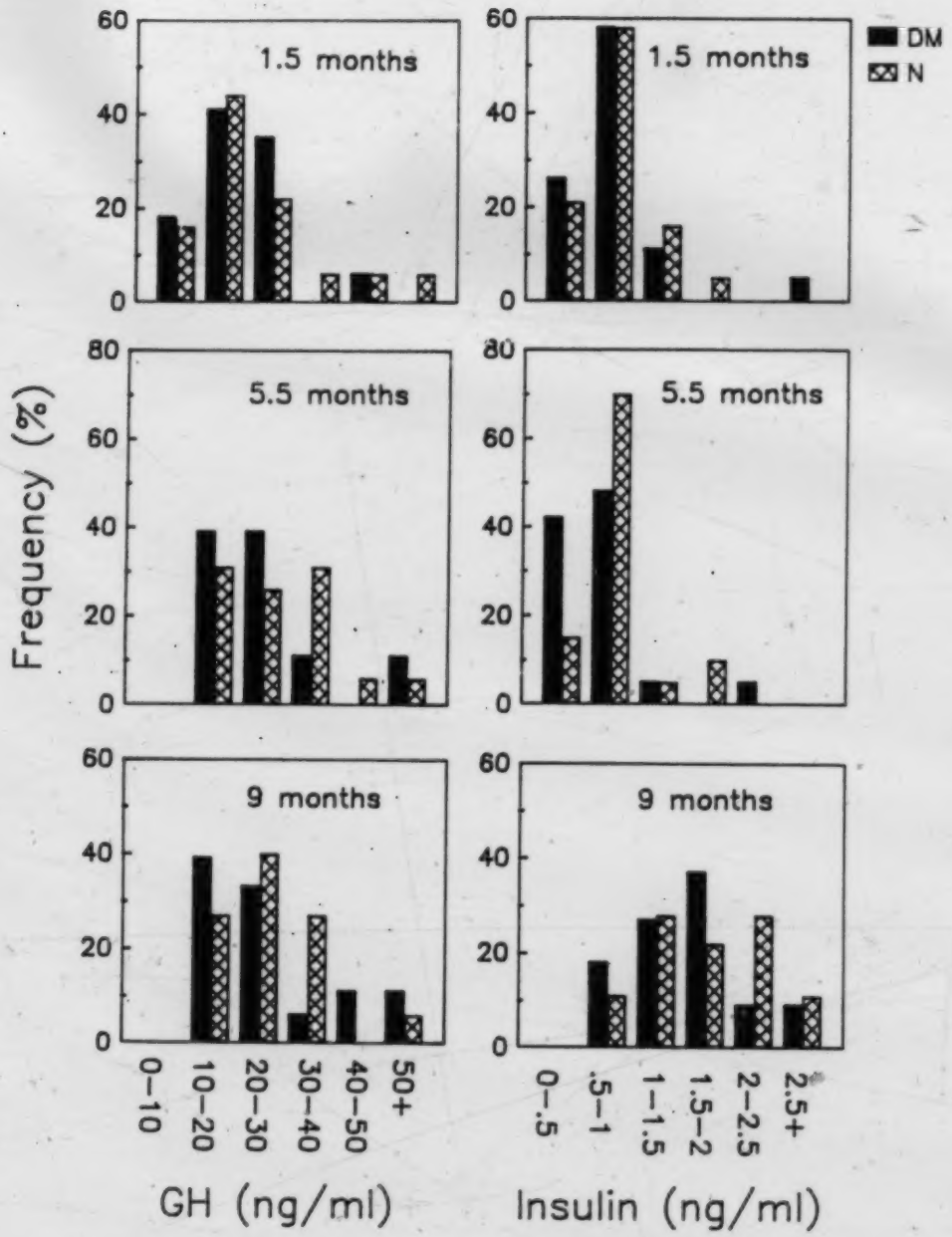

Insulin:GH
Linear and quadratic response, (P<.001)
DM
N
Insulin (ng/ml)
Linear and quadratic response, (P<.0001)
GH (ng/ml)
Linear response, (P<.05)
Age (months)

Figure VII.2. Distribution of plasma growth hormone (GH) and insulin concentrations at the start (1.5 months), middle (5.5 months) and end (9 months) of the experimental period for double-muscled (DM) and normal (N) bull calves.


1.5 months
1.5 months
DM
N
5.5 months
5.5 months
9 months
9 months
Frequency (%)
0
20
40
60
80
0–10
10–20
20–30
30–40
40–50
50+
0–.5
.5–1
1–1.5
1.5–2
2–2.5
2.5+
GH (ng/ml)
Insulin (ng/ml)

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VIII. GENERAL DISCUSSION

While the higher incidences of calving difficulty and perinatal calf mortality in double muscled (DM) cattle are well documented, the first study (Chapter II) provides more evidence on the specific factors which could be responsible for the higher incidences of these traits. Two major factors were identified in this study as contributing to the higher incidence of calving difficulty in these cattle. The first is the conformation of the calf. Although in normal cattle populations the influence of calf conformation on dystocia is minimal after calf weight has been considered (Meijering, 1984), in DM cattle, hypertrophy of the muscles of the hind quarters increases the width of the DM calf making delivery of the fetus difficult. This supports the findings of Vissac et al. (1973) and Hanset and Jandrain (1979). The other major factor identified was the size of the pelvic opening. At similar body weight and age of dam, DM cows had significantly lower values for all pelvic opening measurements. The smaller size of the pelvic opening in DM cows has been attributed to the reduction in size of the pelvic girdle plus a convergence of the iliac branches of the pelvis (Vissac, 1968). The excessive development of the muscles around the pelvis has also been implicated. The contributions of the genotype of the calf and that of the breed group of the dam to the problem of dystocia appear to be equal since the magnitude of the direct effects and that of the maternal effects (Chapter III) were equal.

Significantly higher incidence of perinatal mortality was observed among progeny from DM x DM matings than those from normal (N) cows.

The higher mortality rate could be attributable mainly to the higher incidence of calving difficulty and to some extent the occasional occurence of DM calves with deformities such as enlarged tongues. The genotype of the calf appears to be the only contributing factor, given the higher and significant value for direct effects and the very low and non significant value for maternal effects for this trait (Chapter III).

Reduced fertility in DM cattle as reflected in the calf crop traits was demonstrated in the second study (Chapter III). Both DM males and females have been reported to be responsible for this subfertility (Menissier, 1982a). The contribution of maternal effects to this problem appears to be smaller than that of direct effects. This result implies that an improvement in the fertility of the DM bulls will greatly improve the overall fertility of DM cattle.

Growth rate in DM cattle was lower than in N cattle. This is in agreement with results obtained by other researchers using DM cattle from British breeds (Nott and Rollins, 1979; Geay et al., 1982). The contribution of maternal effects to growth was either small or non significant. Direct effects were responsible for the reduced rate of gain in DM cattle. This implies that selection of DM sires based on conformation, as well as on growth rate could improve growth in DM progeny.

DM carcasses had higher values for all traits dealing with muscling, and lower values for traits dealing with fatness, when the data were evaluated at a constant weight or at a constant age (Chapter IV). This indicates that there are important genetic factors involved other than weight and age differences. These results on carcass

characteristics were similar to those reported by Geay et al. (1982) and Shahin and Berg (1985). The major contributing factor was direct transmitted effects. Maternal effects were unimportant for carcass traits.

Significant heterosis was obtained for most of the traits, suggesting that significant favourable gains can be made, especially in muscling and leaness traits, by crossing DM and N cattle. Maternal effects were generally unimportant for growth and carcass traits, indicating that either of the reciprocal crosses will yield favourable results in growth and carcass composition. However, whereas N x DM matings resulted in higher incidence of calving difficulty compared with DM x N matings, DM x N matings resulted in a lower calf crop. It might be easier to improve calf crop traits in DM x N matings through the use of fertile DM bulls by artificial insemination, than to reduce calving difficulty in the N x DM matings. As well, it might be cheaper to maintain N instead of DM breeding cows. Therefore the use of DM sires on N females may be a reasonable approach in the attempt to utilize the desirable characteristics of DM cattle.

Using this recommended breeding strategy it was observed that carcasses of progeny from DM x N matings (DMx) had higher lean meat yield than N carcasses (Chapter V). Similar results had been obtained by Rollins et al. (1980). The magnitude of the difference, however, differs across carcass grades. The percentage differences in percent muscle, based on rib joint dissection, between DMx and N carcasses grading A1 and A2 were 8.8 and 5.7, respectively. The current Canadian beef grading system is not designed to recognize superior muscling. Increasing consumer demand for leaner meat may result in change of

carcass pricing in favor of leaner carcasses in the future. Under market conditions in which leaner carcasses command premium price, the potential economic benefit of this breeding strategy would be realized.

Although the inheritance of the DM syndrome is speculated to be under the control of a major gene, with modifier genes affecting its expression, the nature and location of this gene is not known (Menissier, 1982b). With current advances in gene transfer techniques in laboratory animals (Palmiter et al. 1982, 1983), identification of this naturally occurring DM gene(s) may be of benefit in the future as these techniques in laboratory animals are being applied to farm livestock. Results from Chapter VI suggest that the growth hormone and the insulin-like growth factor II genes may not be involved in the DM syndrome. Although differences in circulatory levels of growth hormone were found between DM and N animals, these differences were a reflection of differences in growth rate and body weight rather than the degree of muscling (Chapter VII). Similar conclusions were obtained in a study by Michaux et al. (1981). These studies lend further credence to the suggestion by Lawrie et al. (1964) that growth hormone might not be directly involved in the DM syndrome. Circulating levels of insulin were lower in DM compared to N cattle and this finding is consistent with the reduced degree of fatness in DM cattle. As further investigations at the molecular level are considered, the insulin gene could be examined.

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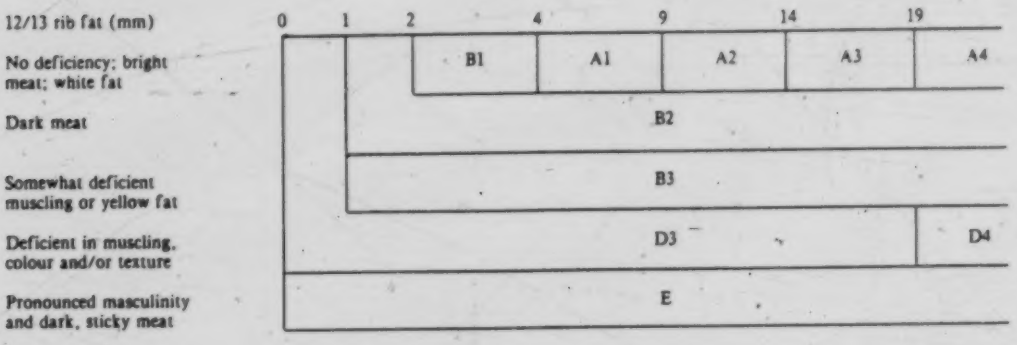
APPENDICES

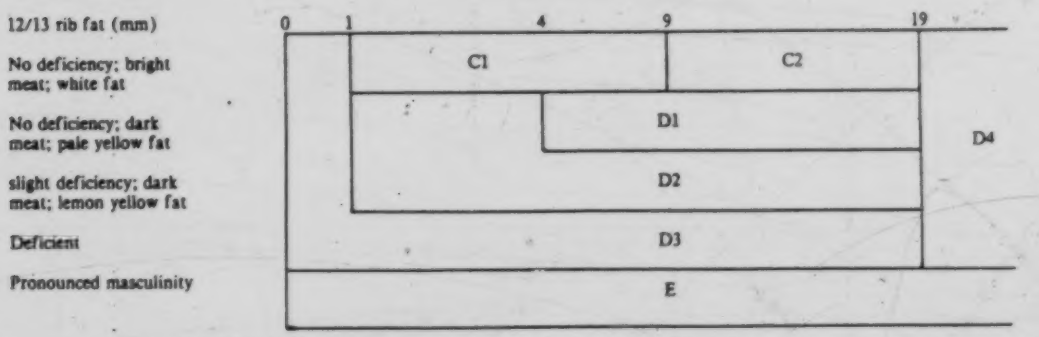
APPENDIX V.1. Specifications for Canada's beef carcass grading regulations.

[After Price, M.A. 1985. Meat carcass grading in Canada. Meat Probe 2:1.]

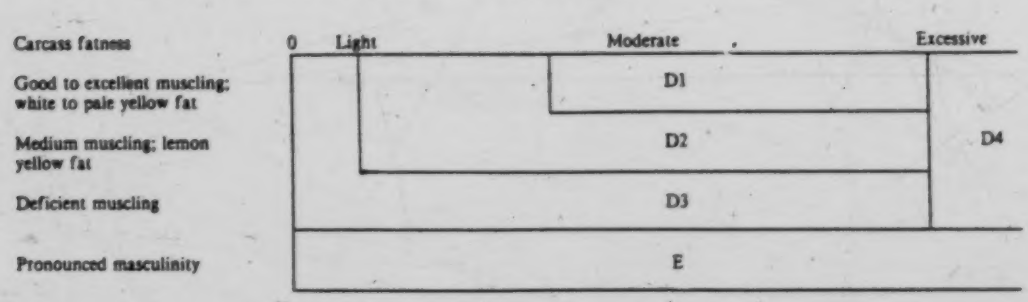
MATURITY I (YOUTHFUL) CARCASSES



MATURITY II (INTERMEDIATE) CARCASSES



MATURITY III (MATURE) CARCASSES



APPENDIX VI.1. Procedures for DNA extraction, DNA digestion and electrophoresis, probe labelling and hybridization.

[Culled from Bork et al. 1989. Can. J. of Zool. (Submitted)]

To facilitate the extraction of DNA, white blood cells were isolated and subsequently lysed. To isolate white blood cells, 5 volumes of a 0.155 M NH_4Cl/0.17 M Tris solution (prewarmed to 37°C) was added to 1 volume of whole blood. Following a 5 min incubation at 37°C, the solution was centrifuged at 2000 rpm for 10 min. After aspiration of the supernatant, the pellet was resuspended in 10 ml of a 0.85% NaCl solution and centrifuged at 2000 rpm for 10 min. This sequence of aspiration, resuspension in 0.85% NaCl, centrifugation and aspiration was then repeated. The white blood cells in the final pellet were then lysed by resuspending this pellet in 2 ml of 100 mM Tris (pH 8.0)/1 mM EDTA and then immediately injecting 2ml of 100 mM Tris (pH 8.0)/40 mM EDTA/1.2% SDS.

For extraction of DNA, an equal volume of TE-saturated phenol was added to the solution of lysed cells and mixed for 10 min. The resulting emulsion was then centrifuged at 5000 rpm for 5 min. After centrifugation, the upper aqueous phase was re-extracted with an equal volume of TE-saturated phenol. This second phenol extraction was followed by an extraction with an equal volume of 1:1 phenol/chloroform and, subsequently, with an equal volume of 24:1 chloroform/isoamyl alcohol. The final aqueous phase was then dialysed against 3 changes of TE over a 24 hour period. Following dialysis, DNA was ethanol precipitated and resuspended in 10 mM Tris Cl (pH 8.0)/ 1 mM EDTA (pH 8.0).

Addition of the restriction enzymes were carried out over 6 h and total digestion time ranged between 18 and 22 h. The digested DNA were electrophoresed on 0.7% agarose gels in a 0.04 M Tris-acetate/0.001 M EDTA (Maniatis et al., 1982) buffer at 30 v for 20 to 24 h. Ethidium bromide (0.3 ug/ml) was added to the gel to allow visualization of DNA. Each gel included DNA markers of known fragment sizes: Bacteriophage lambda cleaved with Hind III, pBR322 cleaved with Sau3A I as well as high molecular weight (HMW) (BRL) marker. The size of the marker fragments ranged from 48 kb to 0.36 kb to allow for an estimation of fragment size of DNA samples. The restricted DNAs were transferred onto a nylon membrane (GeneScreen Plus, New England Nuclear Research Products, Boston MA). Treatment of the DNA before and after transfer to the membrane followed the conditions recommended by the supplier. Method of transfer followed the protocol outlined by Maniatis et al. (1982). Transfer was carried out for 38 to 48 h.

Plasmids containing the cDNA probes used were transformed into appropriate host bacterial strains, isolated, and purified following the procedures outlined by Maniatis et al. (1982). Inserts were cleaved from plasmids by restriction enzyme digestion and separated from vector DNA on LMP agarose (BRL) gels. Probes were radiolabelled with [^{32}P]dCTP (ICN) by the random primer method (Feinberg & Vogelstein, 1983, 1984). The labelled probe fragments were separated from the unincorporated radionucleotides by spun column chromatography (Maniatis et al., 1982). Prehybridization, hybridization and washing of the membrane followed the formamide procedure recemmended by the supplier (Dupont). Membranes were autoradiographed at -70°C using two sheets of Kodak GBX-2 film (Eastman Kodak Co., Rochester, NY) and

Lightning Plus intensifying screens (Dupont). Films were exposed for 3 to 14 days depending on probe activity.

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